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PRIMITIVE *FUSULINELLA* FROM SOUTHERN MISSOURI

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ABSTRACT—Two fusulinids that were obtained from limestones which partly fill a depression or sink in Mississippian limestone near Carterville, Jasper County, Missouri are described and illustrated as *Fusulinella clarki*, n. sp., and *F. searighti*, n. sp. These are primitive forms of *Fusulinella* and are more or less transitional in development between *Profusulinella* and *Fusulinella*. They seem to indicate that the rocks which fill the depression are of about the same age as the lower part of the Mud Springs group of New Mexico, the basal Big Saline limestone of Texas, and some rocks of southern Oklahoma.

MISSISSIPPIAN limestones are present at the surface over a large part of southwestern Missouri, and numerous depressions have developed in them locally. Some of the depressions are filled with Pennsylvanian rocks which occur as outliers. Some of the outliers are considerable distances from continuous outcrops of Pennsylvanian rocks. One of these depressions located near Carterville in the SE¼, NE¼, sec. 20, T. 28 N., R. 32 W., Jasper County is of particular interest for it contains several lithologic units of the typical Pennsylvanian "cycle," including fossiliferous limestones, dark shale, and coal.

This depression was excavated for mining purposes many years ago, and the excavation passed through several feet of chert gravel and penetrated light gray finely granular to coarsely granular crinoidal limestone, black fissile shale, and bituminous or canneloid coal. The excavation has since been covered over, and bed-rock of the depression is no longer exposed. However, the locality was visited by Dr. E. L. Clark a number of years ago when the rocks in the sink were exposed, but the exact order and thickness of these lithologic units were not recorded at that time.

Abundant fusulinid Foraminifera were brought to the surface by the earlier excavations, and numerous specimens were sent to me for study by Dr. W. V. Searight and Dr. Clark. These foraminifers seem diagnostic and permit us to date with considerable accuracy the relative age of the limestone portion of the depression filling. The entire depression or sink fillings were drilled recently by the Missouri Geological Survey, and the recovered core shows 16 feet of Pennsylvanian limestone with abundant fusulinids throughout. Samples from throughout the core have been made available to me. Two fusulinids will be treated in this paper, for they seem to date accurately all of the limestone filling. One of these forms is from 14 feet below the top of the limestone, and the other is from the upper one foot and from the earlier excavation made a number of years ago. These fusu-

linids have proved of such interest that I am describing and illustrating them below and am including for comparison illustrations of several somewhat similar fusulinids found in Oklahoma, Texas, Wyoming, and New Mexico.

These fusulinids belong to two undescribed primitive forms of the genus *Fusulinella* Möller for which I am proposing the names *F. clarki*, n. sp. and *F. searighti*, n. sp. No form of *Fusulinella* has been reported previously for the Pennsylvanian of Missouri, and no form of *Fusulinella* that is considered to be as primitive as these has been described from any part of the Midcontinent region north of southern Oklahoma.

Pennsylvanian rocks in continuous outcrops, commonly referred to the Cherokee shale (Desmoinesian), are present about 10 miles to the north and northwest of the depression from which *Fusulinella clarki*, n. sp., and *F. searighti*, n. sp., were obtained. No fusulinids or other common marine fossils have been found near the base of the Cherokee of southwestern Missouri and southeastern Kansas, and the relative ages of these beds have not been determined closely. Newell (1937) correlated on lithologic evidence the basal Pennsylvanian beds of southeastern Kansas with rocks generally assigned to the lower Desmoinesian McAlester shale farther south in Oklahoma.

More than ten years ago E. N. K. Waering, T. G. Roberts, and M. L. Thompson obtained fusulinids from limestones exposed about three miles west of Pryor, Oklahoma which have been correlated by various individuals with the Sam Creek limestone or the Spaniard limestone (both Desmoinesian in age). However, these fusulinids are referable to *Fusulinella*, one specimen of which is here illustrated (pl. 41, fig. 22). The exact structural relationships of the *Fusulinella*-bearing rocks west of Pryor are not clearly understood. It seems possible that they occur there as down-faulted and eroded blocks below the overlying Desmoinesian. Typical Desmoinesian fusulinids have not been found immediately above the *Fusulinella*-bearing rocks west of Pryor but are found considerably higher in the section. The next nearest *Fusulinella* to the south of Jasper County, Missouri that I have is from a collection obtained by Roberts and Thompson in 1943 from about 3 miles east of Fort Gibson, Oklahoma, where *Fusulinella*-bearing rocks rest directly on Wapanucka limestone.

Skinner (1931) was the first to describe a *Fusulinella* from North America. Thomas (1931) described another species of the genus the same year and from the same locality but from only slightly higher in the section exposed in the Llano uplift of Texas. *Fusulinella* has since been described from numerous localities in America, including the lower part of the Cherokee shale of Iowa (Thompson, 1934), the lower part of the Barnett Hill shale at Barnett Hill and neighboring areas of southern Oklahoma (Thompson, 1935), the basal Hartville limestone of Wyoming and the basal Minnelusa limestone of South Dakota (Thompson, 1936), the Mercer limestones of Ohio (Thompson, 1936), the lower part of the Carbondale formation of Illinois (Dunbar and Henbest, 1942), the Hells Canyon formation of Colorado (Thompson, 1945), and the Mud Springs group of the Derryan of New Mexico and extreme western Texas (Thompson, 1948). Of the numerous forms described from these various stratigraphic units, those from Iowa, Ohio, and Illinois, and possibly those from Colorado, are considered to be lowermost Desmoinesian in age. Most of those from the other areas seemingly are of upper Derryan (Atokan) age.

The rocks which contain *Fusulinella* in New Mexico, extreme western Texas, north-central Texas, and southern Oklahoma are underlain by Pennsylvanian rocks which contain forms of the genus *Profusulinella* Rauser-Cernoussova and Beljaev, a genus considered ancestral to *Fusulinella*. Forms more or less transitional between *Profusulinella* and *Fusulinella* are found in New Mexico, extreme western Texas, north-central Texas and eastern Wyoming as represented by such species as *F. fugax* Thompson from New Mexico and extreme western Texas (pl. 41 fig. 21), *F. primaeva* (Skinner) from north-central Texas (pl. 41, fig. 23), and *F. velmae* Thompson (pl. 41, fig. 24) and *F. protensa* Thompson, both from eastern Wyoming. *Fusulinella clarki*, n. sp., and *F.*

searighti, n. sp. also seem to be somewhat transitional in development between *Profusulinella* and *Fusulinella*.

Profusulinella fittsi Thompson (pl. 41, figs. 13–20) is abundant about 100 feet above the Wapanucka limestone in southern Oklahoma in the region of Barnett Hill and at numerous places immediately to the north and west of there. *Fusulinella prolifica* Thompson is abundant about 100 feet still higher in the section at Barnett Hill and in neighboring areas. No form of *Fusulinella* considered quite as primitive as *F. clarki* and *F. searighti* has been found at Barnett Hill, but it is considered probable that the rocks or geologic interval between *P. fittsi* and *F. prolifica* at Barnett Hill is closely equivalent in age to the limestone in the depression in Jasper County, Missouri. *F. clarki* and *F. searighti* are so closely similar in general development to *F. primaeva* (Skinner) from the basal Big Saline limestone of Texas, *F. fugax* Thompson from the basal part of the Mud Springs group of New Mexico, and *F. velmae* Thompson from the basal part of the Hartville limestone of eastern Wyoming that it is concluded the rocks at these widely separated localities are approximately the same age as the limestones in the depression near Carterville.

It seems evident that southwestern Missouri and neighboring areas were covered by middle Derryan seas. Rocks laid down in this seaway may have been largely removed prior to early Desmoinesian deposition, excepting for local areas where they were in depressions and were protected from erosion. Without more detailed information regarding the structural attitude of the rocks which fill the depression, it does not seem possible to arrive at a logical explanation of the manner or exact time in which the Derryan rocks attained their position in the depression.

I wish to take this opportunity to express my thanks to the several individuals who have helped with this study. Dr. E. L. Clark discovered the fusulinids in the Jasper County depression and made the first collections from there. Dr. W. V. Searight kindly sent the collections to me for study and has furnished information concerning the stratigraphy of the rocks filling the depression. Wm. E. King, Walter L. Moore, and George A. Sanderson have helped me with the technical work connected with this study. Financial aid for completion of this study was furnished by the Research Committee of the University of Wisconsin from funds furnished by the Wisconsin Alumni Research Foundation.

FUSULINELLA SEARIGHTI Thompson, n. sp.
Plate 42, figures 1–7

The shell of *Fusulinella searighti*, n. sp., is small in size and elongate fusiform in shape; with convex to slightly concave lateral slopes, pointed polar ends, and almost straight axis of coiling. Larger specimens of six to seven volutions are 2.5 to 3.3 mm. long and 0.9 to 1.2 mm. wide, giving form ratios of 2.8 to 3.3. The inner three volutions are short and inflated, but the shell becomes elongate fusiform in the outer three or four volutions. Averages of the form ratios of the first to the seventh volution of four specimens, including the holotype, are 1.4, 1.5, 1.8, 2.3, 2.6, 2.9, and 3.0, respectively. The shell is about symmetrically coiled throughout all volutions.

The proloculus is small and has an outside diameter of 71 to 124 microns, averaging 95 microns for seven specimens. The chambers are lowest above the tunnel, and they increase in height slowly poleward but increase sharply near the poles. Averages of the heights of the chambers above the tunnel in the first to the seventh volution of seven specimens are 36, 48, 56, 68, 89, 109, and 139 microns, respectively.

The spirotheca is thin. It is composed of a tectum and upper and lower tectoria in the inner four or five volutions but contains a thin diaphanotheca near the center of the shell in the outer one or two volutions.

The septa are closely spaced. Averages of the septal counts of the first to the sixth volution of three specimens are 11, 18, 19, 22, 25, and 30, respectively. They are fluted in the end thirds of the shell but seem to be unfluted in the central part of the shell.

The tunnel is very narrow in the inner volutions, and it becomes moderately wide in the outer volutions. Its path is slightly shifting in the inner volutions and is even more irregular in outer volutions. Averages of the tunnel angles in the third to the sixth volution of four specimens are 21, 22, 25,

TABLE OF MEASUREMENTS OF *Fusulinella searighti* (in millimeters)

Specimen	L.	W.	Ratio	Diam. prol.	Height of volutions						
					1	2	3	4	5	6	7
A	3.2	1.0	3.2	.063	.023	.035	.052	.054	.088	.135	.142
B	3.3	1.2	2.8	.071	.027	.027	.043	.062	.090	.118	.135
C	3.0	0.9	3.3	.091	.038	.059	.065	.070	.100	.090	—
D	2.5	0.9	2.8	.098	.038	.051	.057	.070	.080	.102	—
E	—	1.1	—	.124	.040	.056	.056	.058	.088	.101	—
F	—	0.7	—	.117	.051	.059	.061	.078	—	—	—
G	—	0.6	—	.100	.032	.050	.038	.085	.085	—	—

Specimen	Form ratio of volutions						
	1	2	3	4	5	6	7
A	1.3	1.7	1.5	2.1	2.4	2.9	3.2
B	1.3	1.4	1.7	1.7	2.5	2.6	2.8
C	1.6	2.1	2.3	3.3	3.2	3.3	—
D	1.3	1.4	1.8	2.0	2.3	2.8	—

Specimen	Septal count						Tunnel angle (degrees)				
	1	2	3	4	5	6	2	3	4	5	6
A	—	—	—	—	—	—	13	21	20	25	37
B	—	—	—	—	—	—	—	21	25	28	33
C	—	—	—	—	—	—	—	21	24	29	31
D	—	—	—	—	—	—	—	19	21	20	28
E	11	18	21	22	25	30	—	—	—	—	—
F	12	21	20	26	—	—	—	—	—	—	—
G	11	16	17	19	—	—	—	—	—	—	—

(Specimens A, B, E, F, and G are illustrated by figures *4*, *3*, *6*, *7*, and *5*, respectively, on Plate 42. Specimen A is the holotype .

and 32 degrees, respectively. The chomata are high and asymmetrical, with steep tunnel sides and low lateral slopes. They extend completely to the polar ends in the inner four to five volutions but become narrower in the outer volutions. The chomata are highest adjacent to the septa, and at least in the tunnel area they extend up the septa to the top of the chambers and spread onto the lower surface of the spirotheca.

Remarks.—The thin diaphanotheca of *Fusulinella searighti* and its occurrence only

EXPLANATION OF PLATE 41

All illustrations on this plate are of unretouched photographs.

FIGS. *1–12*—*Fusulinella clarki*, n. sp. *1*, *6*, Axial section of the holotype; *2*, *3*, *5*, *7–10*, *11*, axial sections of paratypes; *4*, *12*, sagittal section of a paratype. *1–4* are ×40 and all others are ×20. Jasper County, Missouri (M-38). (p. 325)

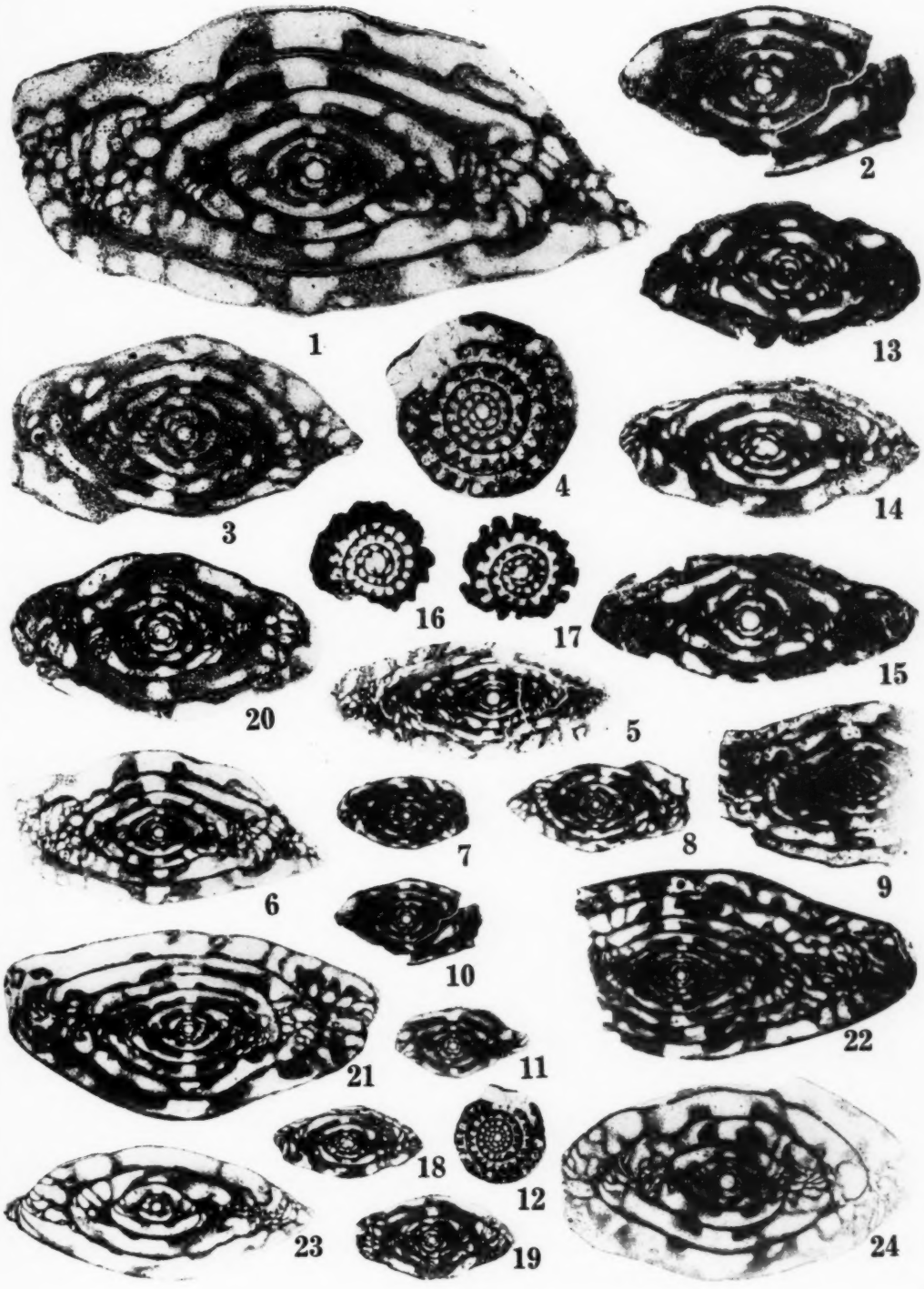
13–19—*Profusulinella fittsi* (Thompson). *13–15*, *18*, *19*, Axial sections of topotypes; *16*, *17*, sagittal sections of topotypes. *13–17* are ×40 and all others are ×20. About 100 feet above the Wapanucka limestone. Center NW¼, sec. 10, T. 1 N., R. 8 E., Coal County, Oklahoma (O-126). (p. 323)

20—*Fusulinella fugax* Thompson. Axial section of a paratype, ×20. Fra Cristobal formation, New Mexico. (p. 323)

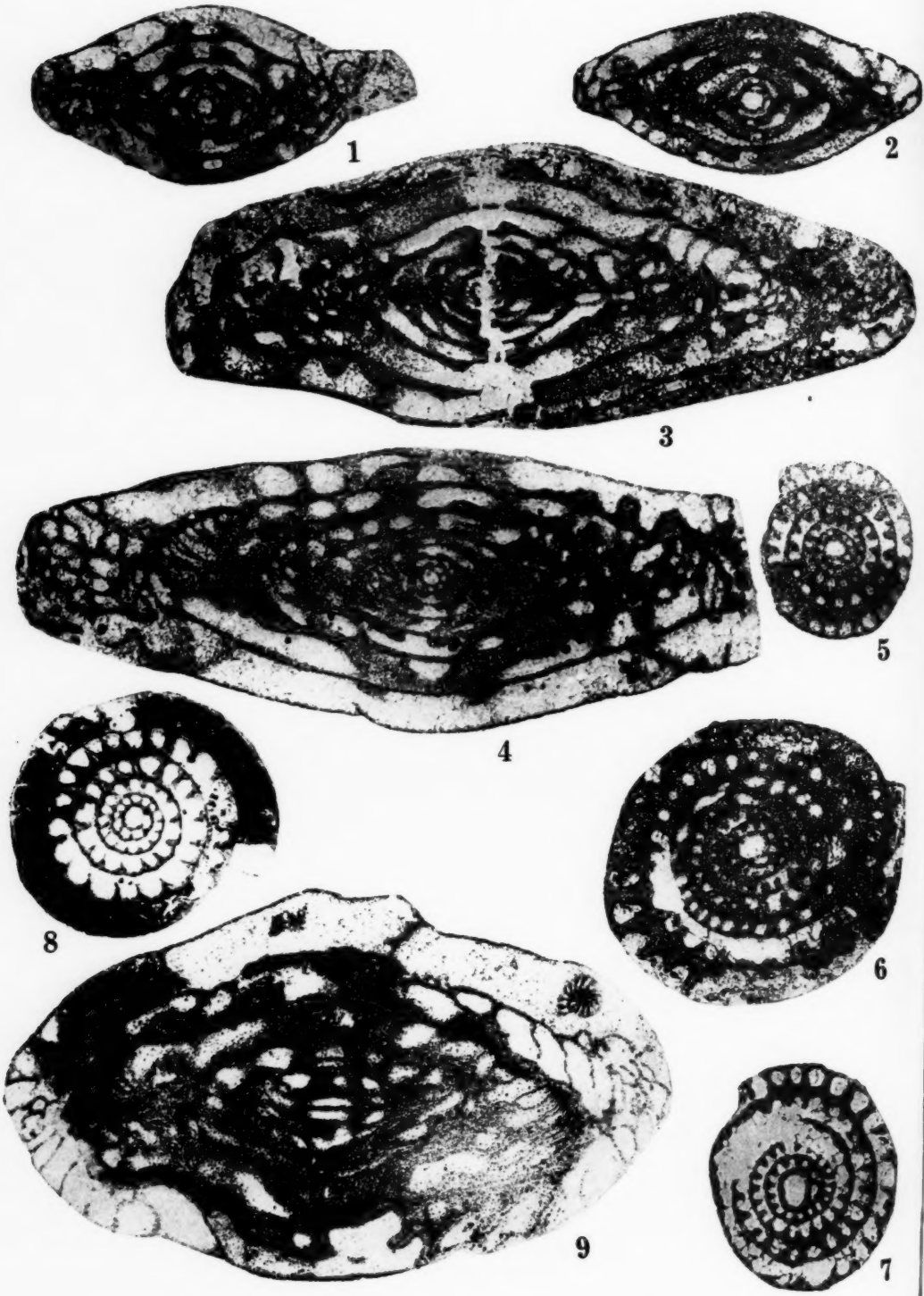
21—*Fusulinella* aff. *F. devexa* Thompson. Axial section, ×20. Three miles west of Pryor, Oklahoma (O-46). (p. 322)

22—*Fusulinella? primaeva* (Skinner). Axial section of a syntype, ×20. Base of Big Saline limestone, Texas. (p. 323)

23—*Fusulinella velmae* Thompson. Axial section of a syntype, ×20. Lower Hartville limestone, Wyoming. (p. 323)



Thompson, primitive *Fusulinella* from Missouri



Thompson, primitive *Fusulinella* from Missouri

in the outer volutions of mature shells strongly suggest that this form is a primitive representative of the genus. The general nature of the septal fluting, massive chomata, and thin diaphanotheca of this species and of *F. clarki*, n. sp., described below resemble very closely those features of *Fusulinella bocki* Möller from Russia. This resemblance is particularly striking between *F. clarki* and *F. bocki*.

Fusulinella searighti resembles *F. dakotensis* Thompson, 1936, somewhat closely except that its shell is smaller, is more inflated, has thinner spirotheca, has more massive chomata, and has a more narrow tunnel than the latter form.

Fusulinella searighti can be distinguished from *F. clarki*, n. sp., by its shorter shell, relatively more inflated shell, relatively higher chambers, more sharply pointed poles, and broader chomata.

This species is named in honor of Dr. Walter V. Searight who sent me the collections and who furnished information concerning their occurrence.

Occurrence.—*Fusulinella searighti* is very abundant about 14 feet below the top of the limestone which fills the depression or limestone sink near Carterville, Missouri. It is associated with abundant *Millerella*. This form seemingly has a considerable distribution in the lower part of the depression filling, but its range has not been determined fully.

FUSULINELLA CLARKI Thompson, n. sp.
Plate 41, figures 1–12; plate 42, figures 8, 9

The shell of *Fusulinella clarki*, n. sp., is small in size and inflated fusiform in shape; with almost straight axis of coiling, convex lateral slopes, and bluntly pointed poles. Larger specimens of six to six and a half volutions measure about 2.4 to 2.8 mm. long and 0.9 to 1.2 mm. wide, giving form ratios of 2.0 to 2.8. One elongate paratype of five and a half volutions is 2.4 mm. long and 1.1 mm. wide, giving a form ratio of about 2.8. The form ratios of the first to the sixth volution of the holotype specimen are 1.1, 1.5, 1.8, 2.2, 2.4, and 2.5, respectively. Form ratios of the first to the fifth volution of the above mentioned elongate paratype specimen are 1.4, 1.8, 2.3, 2.9, and 2.9, respectively.

The proloculus is relatively large and has an outside diameter of 66 to 116 microns, averaging about 79 microns. The shell expands about uniformly. The heights of the chambers above the tunnel in the first to the sixth volution of the holotype are 38, 53, 70, 97, 131, and 160 microns, respectively. The heights of the chambers in the first to the seventh volution of a typical paratype specimen are 43, 48, 58, 73, 111, 131, and 140 microns, respectively. The chambers are lowest above the tunnel where the above measurements were made, and they increase in height rather uniformly toward the poles and very sharply in the extreme polar ends.

The spirotheca is composed of the tectum and upper and lower tectoria in the inner four and a half volutions and has a thin diaphanotheca below the tectum in the tunnel area of the outer volutions. The tectum and diaphanotheca measure about 10, 13, and 18 microns in the fourth to sixth volution, respectively.

The septa are composed of the tectum and thick deposits on both sides. They are slightly fluted in the extreme polar ends but are about plane across the central part of the shell. The septal counts of the first to the fifth volution of a typical paratype are 8, 13, 15, 20, and 26, respectively.

The tunnel is narrow, and its path is irregular. Averages of the tunnel angles of the second to the fifth volutions of six

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EXPLANATION OF PLATE 42

All illustrations on this plate are unretouched photographs, and all of them are magnified ×40.

FIGS. *1–7*—*Fusulinella searighti*, n. sp. *1–3*, Axial sections of paratypes; *4*, axial section of the holotype; *5–7*, sagittal sections of paratypes. All from 14.0 to 14.5 feet below the top of the limestone filling of the depression or sink in southwestern Missouri. (p. 323)

8, 9—*Fusulinella clarki*, n. sp. *8*, Sagittal section of a paratype; *9*, tangential section of a paratype. Both from the upper one foot of the limestone filling of the depression or sink in southwestern Missouri. (p. 325)

TABLE OF MEASUREMENTS OF *Fusulinella clarki* (in millimeters)

Specimen	L.	W.	Diam. prol.	Thickness of spirotheca		
				4	5	6
1	1.77	0.79	.080	.008	.010	.015
2	1.11	0.52	.063	.010	—	—
3	0.99	0.54	.063	—	—	—
4	1.24	0.62	.073	.007	.011	—
8	—	0.67	.068	.011	.018	—
9	2.44	0.87	.116	.011	—	.014
10	2.80	1.13	.082	.011	.014	.019
11	—	1.17	—	.009	.014	.019

Specimen	Height of volutions						Septal count				
	1	2	3	4	5	6	1	2	3	4	5
1	.034	.039	.058	.060	.082	.131	—	—	—	—	—
2	.027	.043	.053	.073	—	—	—	—	—	—	—
3	.025	.049	.078	.097	—	—	—	—	—	—	—
4	.034	.047	.058	.073	.082	—	—	—	—	—	—
8	.029	.039	.066	.087	.102	—	8	13	15	20	26
9	.040	.058	.073	.097	.111	—	—	—	—	—	—
10	.038	.053	.070	.097	.131	.160	—	—	—	—	—
11	.043	.048	.058	.073	.111	.131	—	—	—	—	—

Specimen	Form ratio of volutions						Tunnel angle (degrees)				
	1	2	3	4	5	6	1	2	3	4	5
1	1.0	1.2	1.5	1.7	1.9	2.2	—	11	12	20	21
2	1.1	1.4	1.6	2.1	—	—	8	11	16	—	—
3	1.0	1.4	1.8	1.8	—	—	—	14	16	—	—
4	1.2	1.5	1.7	1.7	2.0	—	—	—	—	—	—
9	1.4	1.8	2.3	2.9	2.9	—	15	17	20	25	26
10	1.1	1.5	1.8	2.2	2.4	2.5	—	14	16	24	28
11	—	—	—	—	—	—	13	14	18	30	30

(Specimens 1–4, 9–11 are illustrated by figures *3&8*, *11*, *7*, *2*, *4&12*, *5*, *1&6*, and *9*, respectively, on Plate 41. Specimen 10 is the holotype.)

specimens, including the holotype, are 14, 20, 25, and 24 degrees, respectively. The chomata are very massive throughout the shell. They are more than half as high as the chambers midway between the septa but extend to the tops of the chambers immediately adjacent to the septa. Their tunnel sides are vertical to slightly overhanging, and their poleward slopes are very low, with their lateral edges ending near the poles in the second to fifth volutions. In the outer one or two volutions the chomata are more narrow and have steep poleward slopes.

Remarks.—*Fusulinella clarki*, n. sp., is considered to be a primitive representative of the genus. Its first five volutions have a spirothecal structure like that of *Profusulinella* Rauser-Cernoussova and Beljaev, 1936, for they contain only three layers. However, the presence of a diaphanotheca in the outer volutions would indicate that it belongs to *Fusulinella*. This primitive type of wall structure in its early volutions suggests that this species is among the earlier forms of the genus and that it is closely similar in age to *Fusulinella primaeva* (Skinner) from the very base of the type section of the Big Saline limestone of Texas and *F. fugax* Thompson from the basal part of the Fra Cristobal formation of the Derryan of New Mexico. However, *F. clarki* can be distinguished from these forms by the smaller size of specimens of an equal number of volutions, the more massive chomata than those of *F. primaeva*, and a more elongate shell than that of *F. fugax*.

Fusulinella clarki can be distinguished

from *F. prolifica* by its more inflated and smaller shell, more massive chomata, and the later appearance of the diaphanotheca in its shell. *Fusulinella clarki* can be distinguished from *F. searighti*, n. sp., by its shorter and more inflated shell, more inflated chambers for corresponding parts of the shell, more narrow chomata, and more blunt polar ends.

A large number of small specimens of five to six volutions are associated with the holotype specimen of *Fusulinella clarki* that resemble closely in all measurable features *Profusulinella fittsi* (Thompson), a form which is very abundant about 100 feet above the Wapanucka limestone at and in the region north of Barnett Hill, Oklahoma. The Missouri specimens may be conspecific with *P. fittsi*. However, these smaller specimens, although more closely coiled and shorter than the holotype of *F. clarki*, are here referred tentatively to it.

This species is named in honor of Dr. E. L. Clark, Director of the Missouri Geological Survey, who made the first collection of fusulinids from the Jasper County depression.

Occurrence.—*Fusulinella clarki* is abundant in the upper one foot of the limestone cores obtained from fillings in the depression near Carterville, Missouri, and is abundant in limestone samples brought to the surface by the mining operations of a number of years ago. It is presumed that the mine excavations were principally through the upper few feet of the limestone fillings.

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A FOSSIL SNAKE OF THE GENUS *HETERODON* FROM THE PLIOCENE OF KANSAS

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THE technique of micro-fossil collecting worked out and described by Hibbard (Cont. Mus. Paleo. Univ. Mich., 8 (2), 1949, pp. 7–19, 4 pls.) is rapidly becoming the most outstanding factor in the expansion of our knowledge of the distribution of the smaller animals through time. The number of species of mammals known as fossils from the Pliocene and Pleistocene beds of Kansas has been considerably more than doubled since Hibbard's work began. It was inevitable that his methods would also produce specimens representing other vertebrate groups, and work on some of the bird, amphibian, fish, and lizard remains has already been published. The snake material is extensive and, although it consists primarily of vertebrae, has produced three maxillaries and a palatine which are characteristic of the distinctive snake genus *Heterodon*.

HETERODON PLIONASICUS Peters, n. sp.
Figures 1–6

Holotype.—No. 28113, University of Michigan Museum of Paleontology, a left maxillary. *Paratypes*, No. 28112, a right maxillary, No. 29587, a right maxillary, and No. 28137, a left palatine. All specimens collected by the 1947 and 1951 University of Michigan Museum of Paleontology field parties.

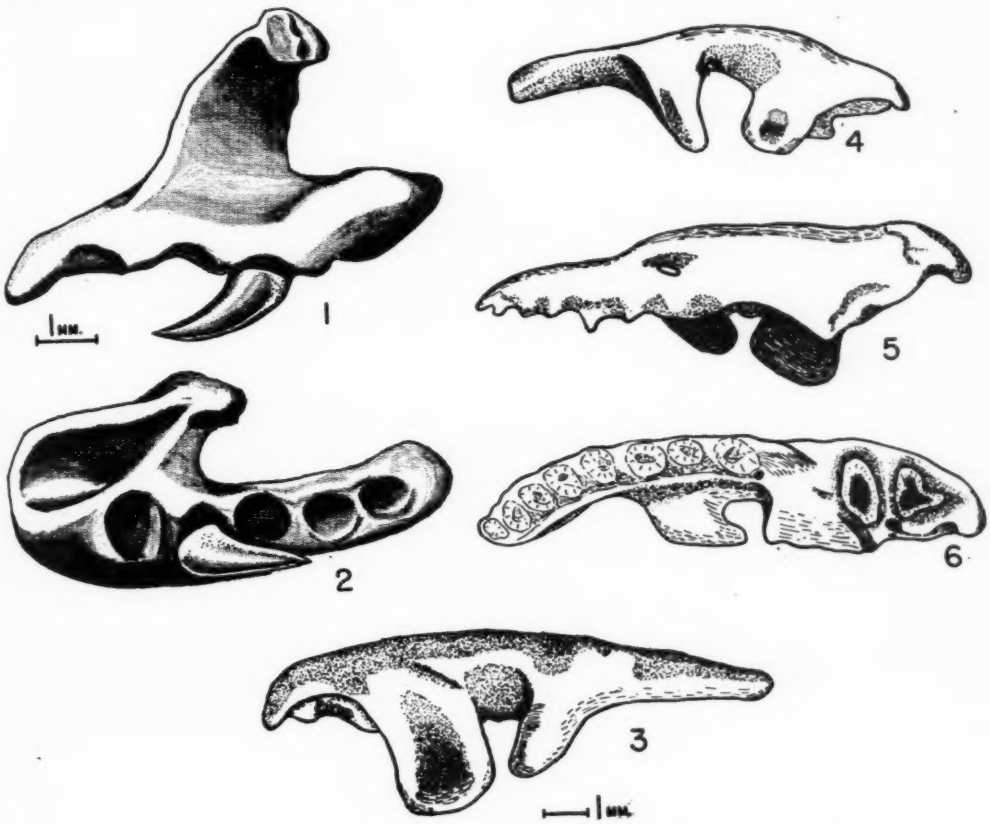
Horizon and type locality.—Upper Pliocene, Rexroad formation, Rexroad fauna. Locality UM-Kl-47, in Fox Canyon, in sec. 35, T. 34 S., R. 30 W., XI Ranch, Meade County, Kansas.

Diagnosis.—A snake belonging to the genus *Heterodon*, very similar in appearance to *Heterodon nasicus*, but reaching a larger size. Differs from *H. platyrhinos* in the close approximation of the internal processes of the maxillary, the greater curvature of the anterior portion of the maxillary, and the presence of fewer teeth on the maxillary. Differs from *H. nasicus* in its greater size, more stout appearance of the maxillary, and the presence of a strong ridge on the labial border of the diastemal area. Differs from *H. simus* in its larger size, stout appearance, less strongly curved prefrontal process, and in presence of a canal for the anterior palatine nerve in the palatine bone (canal absent in *simus*). Differs from all three species in the absence of a well marked shoulder on the dorsal anterior edge of the point of articulation of the external or labial arm of the ectopterygoid with the maxillary.

Description of holotype.—A short, broad, diacranterian bone, with the tips of the prefrontal and ectopterygoid processes closely approximated, bearing eight teeth anterior and two enlarged teeth posterior to the diastema. The entire anterior portion of the maxillary to the diastema exhibits a slight clockwise twist that is directed lingually, and is curved inward, with the strongest arc of the curve bearing five teeth, all anterior to the base of the prefrontal process. A well-defined ridge runs along the lingual aspect of the tooth row, while the tooth sockets form a prominent part of the edge of the labial aspect. A short ridge on the labial aspect arises at the outer margin of the eighth tooth socket and forms a raised border on the diastemal area, directed inward and running to the base of the anterior of the two sockets for the enlarged cranterian teeth. These sockets are about twice as large as those of the precranterian teeth, and are set at a 45° angle to the horizontal plane of the maxillary. A prominent shoulder extends posteriorly and inwardly over the posterior cranterian tooth, and has a downwardly directed tip. The prefrontal process arises on the dorso-lingual aspect at the level of the sixth tooth, and is directed inwardly and slightly down. It tapers evenly; the dorsal surface is rounded; the ventral surface is almost flat; and the areas of contact with the prefrontal are poorly de-

fined. A very weakly indented contact surface on the posterior edge of the outer tip indicates a possible articulation with the palatine. The ectopterygoid process arises on the dorsolingual aspect posterior to and slightly lower than the prefrontal process, at the level of the anterior end of the diastema. The cup-shaped articulatory surface at its dorsal tip for accommodation of the lingual arm of the anterior end of the ectopterygoid extends in a weakly defined fashion to the dorso-labial aspect, where a slightly more prominent indentation indicates the articulatory surface for reception of the labial arm of the ectopterygoid. The posterior edge of the ectopterygoid process forms the inner border of a slight shelf over the anterior cranterian tooth socket. The measurements of the holotype and the two paratypical maxillaries are given in Table I.

Paratypes.—No. 28112, a right maxillary with slightly greater distance between the tips of the lateral processes. The tooth count is uncertain, but there appear to be seven anterior to the diastema. There are two cranterian teeth. The ridge on the outer edge of the diastema is not as prominent as in the type. The prefrontal process is slightly longer and more pointed. No. 29587, a right maxillary with almost the entire portion anterior to the prefrontal process broken off. Two precranterian teeth are still in place. Both have been badly worn during fossilization, but are definitely aglyphous teeth with the tips curving posteriorly. The anterior edge of the tip of the



FIGS. *1–6—1*, lingual view of left palatine, paratype no. 28137; *2*, occlusal view of left palatine, no. 28137; *3*, lingual view of left maxillary, holotype no. 28113; *4*, lingual view of right maxillary, paratype no. 28112; *5*, labial view of holotype; *6*, occlusal view of holotype. (Scale for Fig. 2 as in Fig. 1; scale for Figs. 4–6 as in Fig. 3.)

ectopterygoid process is flared and rolled slightly more than in the type. No. 28137, a left palatine, a short, comparatively broad bone, bore five teeth on its inner edge, only one of which, the second, is still present. The prefrontal process arises at and is continuous with the tip of the inner portion of the bone, and the anterior tip is a gently rounded, broad, flat area. The foramen of the anterior palatine nerve opens into a deep groove at a point opposite the center of the first tooth cavity. The groove is open at the anterior end of the bone, with the outer flared tip of the bone rising sharply anteriorly over it. The posterior opening of the foramen, not visible from below, is above the posterior edge of the second tooth, at which point the bone narrows to the width of the toothed portion and continues posteriorly in a slight arc, directed outwardly. The posterior tip is directed slightly downward. The dorsal process, which forms a portion of the border of the interior nares, arises from the outer edge of the toothed portion. Its base forms part of the posterior opening of the nerve foramen. It rises in a straight line, tipped slightly in, with scant narrowing, for 2.2 mm., at which point a strong arc begins, and the bone is abruptly narrowed to an almost circular cross section. The tip of the process is missing. The outer end of the dorsal surface of the prefrontal process, following a shallow groove for the articulation with the prefrontal, is a definite shoulder followed by a rectangular block of bone directed posteriorly. The measurements of this palatine are as follows (all in mm.): maximum anterior-posterior length, 6.7; maximum width including prefrontal process, 3.0; anterior end to opening of foramen of anterior palatine nerve, 2.0; length of canal of anterior palatine nerve, 1.1; anterior end to first tooth, 1.7; length of tooth row, 4.8; height of dorsal process, 2.2.

Generic assignment.—*Heterodon* is the only genus of snakes known from the Recent of Kansas that possesses a diacranterian maxillary, with the cranterian teeth enlarged and fanglike, although not grooved. In addition, the genus is characterized in the Recent species by an upturned, shovel-like, foreshortened snout and pointed rostral scale. The shortening has resulted in general compression of all the bones on the anterior portion of the skull, with the maxillary reduced in length, curved inward, and bearing few teeth, and the palatine very short, with the anterior end withdrawn to the level of the external or prefrontal process, and also bearing few teeth. This shortened snout does not occur in any other Kansas genera.

TABLE 1.—MEASUREMENTS OF THE HOLOTYPE AND TWO PARATYPE MAXILLARIES OF *Heterodon plionasicus*. ALL MEASUREMENTS IN MILLIMETERS

	28113	28112	29587
Maximum anterio-posterior length	10.5	8.4	—
Length of diastema	1.7	1.4	0.9
Minimum distance between lateral processes	0.4	0.7	0.6
Maximum width of ectopterygoid process	2.1	1.3	0.9
Length of maxillary anterior to prefrontal process	3.3	2.5	—
Length of maxillary anterior to diastema	6.3	5.6	—
Length of maxillary posterior to diastema	3.4	2.1	1.6

On the other hand, shortening of the snout and development of a shovel-like rostral has taken place in many diverse genera and on practically every continent inhabited by snakes, such as *Lioheterodon* on Madagascar, *Lystrophis* in South America, and *Rhamphiophis* in Africa, among others. The general resemblance between the toothed bones of these genera and of *Heterodon* are so great in some that the choice of *Heterodon* as the generic quarters of *plionasicus* is substantiated primarily by geography. The maxillary and palatine of *Lystrophis* differ from those of *Heterodon* in only minor details, with the former having fewer maxillary teeth, a less expanded posterior portion of the maxillary, and a straight or slightly incurved anterior edge on the palatine. The two genera are very closely related, however, and are separated

today upon the basis of paleontologically evanescent characters, as, for example, the number of dorsal scale rows and the presence or absence of keeling on the dorsal scales.

Actually, the similarities between these bones and those of the modern species of *Heterodon* are strong and obvious. The new species is so much like the modern *nasicus* that a direct phylogenetic relationship is hardly questionable.

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SOME LATE OLIGOCENE LARGER FORAMINIFERA FROM PANAMA*

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ABSTRACT—Three species of *Lepidocyclina* and one species of *Miogypsina* (*Miolepidocyclina*) from the late Oligocene of Panama are discussed. A key to the Oligocene species of the subgenus *Lepidocyclina* in the western hemisphere is given. New thin sections of topotype specimens of *Lepidocyclina miraflorensis* Vaughan are illustrated and described.

INTRODUCTION

RECENTLY W. P. Woodring, of the U. S. Geological Survey, sent me five samples from the Panama Canal Zone collected by D. F. MacDonald and T. W. Vaughan in 1911, while the canal was being constructed. In each of these samples there is at least one large Foraminifera in association with mollusks. The U. S. National Museum kindly sent me a small fragment of the type material containing *L. miraflorensis* Vaughan and granted me permission to section any specimens found in this fragment. The locality data are as follows:

USGS loc. 5866—Original line of Panama Railroad, near Tower N. Collected by D. F. MacDonald, 1911.

USGS locs. 6019a, 6019f, 6019g—West side of Gaillard Cut. Collected by D. F. MacDonald and T. W. Vaughan, 1911.

USGS loc. 6255—Half a mile south of Miraflores Station, on the wagon road to Panama. Collected by D. F. MacDonald, 1911.

USGS loc. 6257—Bald Hill, 1 mile southeast of Pedro Miguel and ⅛ mile east of wagon road. Collected by D. F. MacDonald, 1911.

* Publication authorized by the Director, U. S. Geological Survey.

Three accidental equatorial sections of specimens from loc. 6019a, were figured by Cushman (1918, pl. 34, figs. 2, 3a, b) under the name *Lepidocyclina canellei* Lemoine and R. Douvillé. Two accidental equatorial sections from loc. 6019f were figured also by Cushman (1918, pl. 35, fig. 3, and pl. 36) under the name *Lepidocyclina chaperi* Lemoine and R. Douvillé.

The names assigned in this article to the various species present follow:

Loc. 5866—*Lepidocyclina* (*Lepidocyclina*) *miraflorensis* Vaughan, megalospheric individual.

Loc. 6019a—*Lepidocyclina* (*Lepidocyclina*) *waylandvaughani* Cole, megalospheric individuals.

Loc. 6019f—*Lepidocyclina* sp., probably *L. miraflorensis* Vaughan, microspheric generation.

Loc. 6019g—*Lepidocyclina* (*Lepidocyclina*) *miraflorensis* Vaughan, microspheric and megalospheric, one specimen of each.

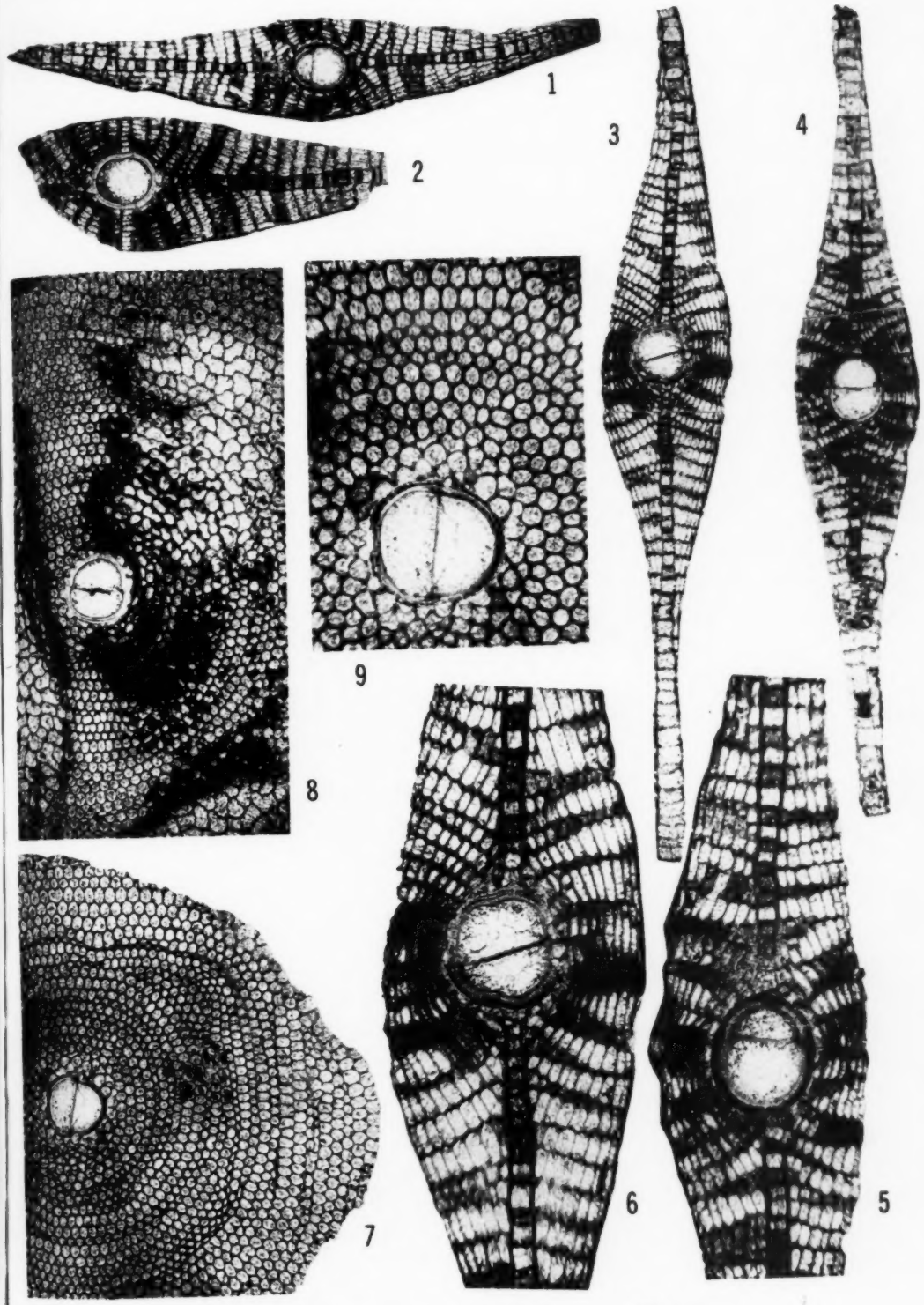
Loc. 6257—*Lepidocyclina* (*Lepidocyclina*) *parvula* Cushman, megalospheric and microspheric individuals; *Miogypsina* (*Miolepidocyclina*) *panamensis* (Cushman).

The stratigraphic position of these samples except 6019g, which represents the Culebra

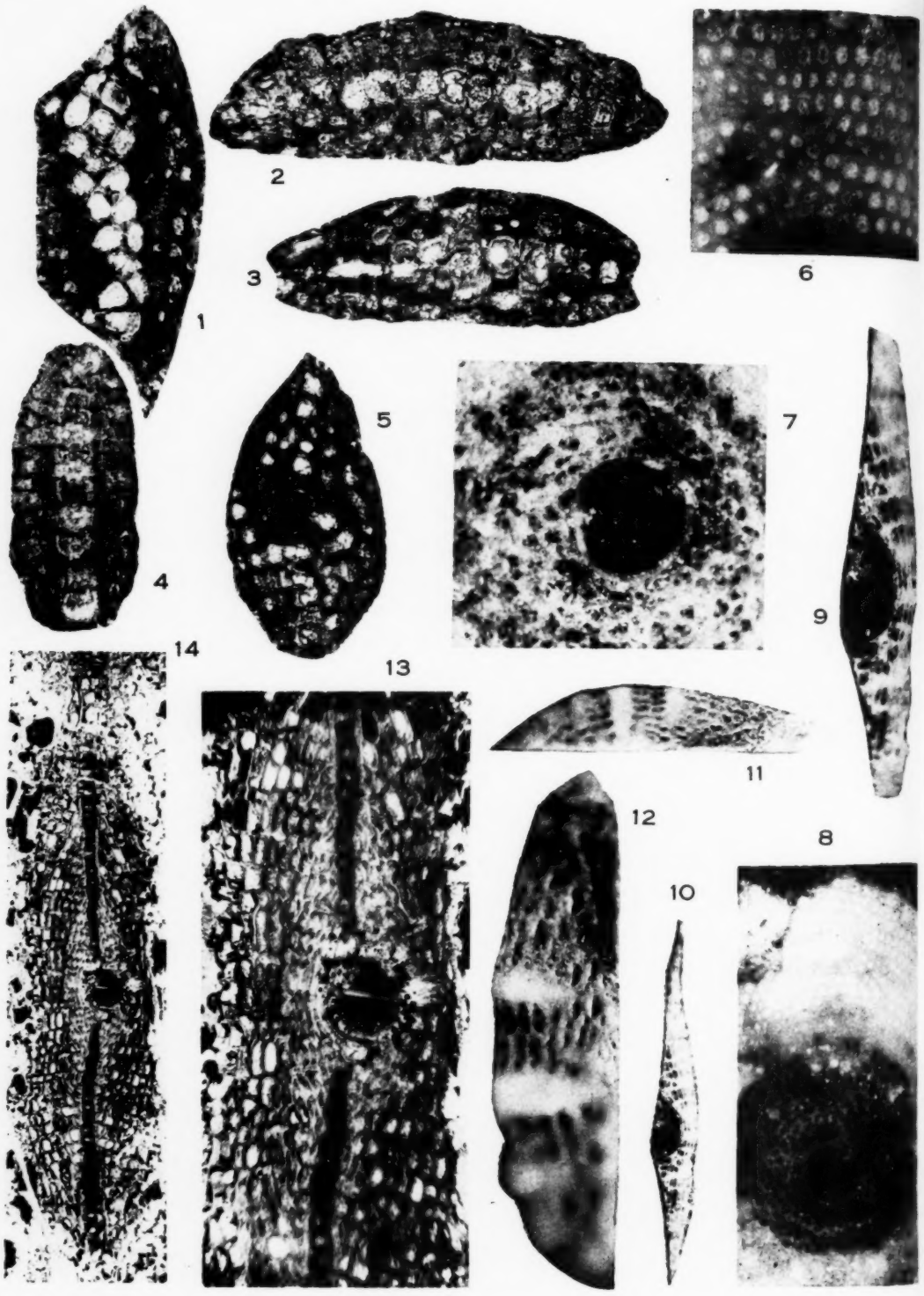
EXPLANATION OF PLATE 43

FIGS. *1–9*—*Lepidocyclina* (*Lepidocyclina*) *miraflorensis* Vaughan. Topotype specimens from USGS loc. 6255. *1–6*. Vertical sections, *1–4*, ×20; *5*, *6*, ×40; *5* is an enlargement of the central portion of *1* and *6* is an enlargement of the central portion of *3*. *7–9*. Equatorial sections, *7*, *8*, ×20; *9*, ×40, *9* is an enlargement of the central portion of *7*. (p. 333)

The expense of the plates has been defrayed by the William L. E. Gurley Foundation for Paleontology of Cornell University.



Cole, Oligocene Foraminifera from Panama



Cole, Oligocene Foraminifera from Panama

formation, was mentioned by Woodring and Thompson (1949). The citation to these samples follows:

USGS loc. 5866 (Woodring and Thompson, 1949, p. 238)—Emperador limestone member of the Culebra formation.
USGS loc. 6019a (idem, p. 238)—Culebra formation.
USGS loc. 6019f (idem, p. 238)—Culebra formation.
USGS loc. 6255 (idem, p. 241)—La Boca formation.
USGS loc. 6257 (idem, p. 241)—La Boca formation.

Woodring (Woodring and Thompson, 1949, p. 246, fig. 2) placed the La Boca formation in the early Miocene and assigned to the Culebra formation a late Oligocene (?) and early Miocene age. They correlated the lower portion of the Culebra formation with the upper member of the Caimito formation. However, they noted (p. 241) that H. G. Schenck on the basis of smaller Foraminifera considered the La Boca formation to be late Oligocene in age, a determination that agrees with the discovery of *Lepidocyclina* and *Miogypsina* in a sample (6257) from the La Boca formation.

However, the possibility must be kept in mind that *Lepidocyclina* and *Miogypsina* may extend into the Miocene in the western hemisphere. There is a similarity in the determination of the age of the La Boca formation to that of the so-called *Miogypsina-Heterostegina* zone of the Anahuac wedge of the Gulf Coast. Gravell and Hanna (1938, p. 989) wrote "Until sufficient opposing evidence is presented, we believe it best to follow established usage and consider the *Heterostegina* zone as a part of the Oligocene."

DISCUSSION OF THE SPECIES

The following key to megalospheric specimens of Oligocene species of the subgenus *Lepidocyclina* was prepared in the study of the specimens in the present collection. As this was found to be very useful it is presented here (*see top of next page*).

Cole (1952, p. 21) considered that the type vertical sections of *L. miraflorensis* were made from specimens of *L. vaughani*. Although both species have long, open cavities to the lateral chambers with very thin roofs and floors, it is clear after studying topotype specimens of *L. miraflorensis* that this species is a valid one. Therefore, a new description of this species based on the topotype specimens is given and the measurements of the specimen from loc. 5866 are subjoined to the tables of measurements to demonstrate its similarity to the topotype specimens of *L. miraflorensis*.

LEPIDOCYCLINA (LEPIDOCYCLINA) MIRAFLORENSIS Vaughan

Plate 43, figures 1–9; plate 44, figures 6–10

1918. *Lepidocyclina vaughani* CUSHMAN, U. S. Nat. Mus. Bull. 103, p. 93, pl. 37, figs. 1, 2, 3, 5 (not *Lepidocyclina vaughani* Cushman, pl. 37, fig. 4, or pl. 38).
1920. *Lepidocyclina vaughani* CUSHMAN, U. S. Geol. Survey Prof. Paper 125, p. 64 (parts).
1923. *Lepidocyclina miraflorensis* VAUGHAN, Proc. Nat. Acad. Sci., vol. 9, p. 257.
1927. *Lepidocyclina* (*Lepidocyclina*) *miraflorensis* VAUGHAN, Proc. U. S. Nat. Mus., vol. 71, art. 8, p. 4, pl. 4, figs. 3–5.

Test of moderate size, composed of a lenticular central area bordered by a relatively wide, thin rim. The rim is demarked sharply from the biconvex central area. The central area has very small papillae more or less evenly distributed over its surface. The papillae at the apex of the central area are

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EXPLANATION OF PLATE 44

FIGS. *1–5*—*Miogypsina* (*Miolepidocyclina*) *panamensis* (Cushman). *1*. Oblique equatorial section showing embryonic and equatorial chambers, ×40; *2–5*. Vertical sections, ×40; *2*, centered, showing embryonic chambers; others off center; loc. 6257. (p. 336)
6–10—*Lepidocyclina* (*Lepidocyclina*) *miraflorensis* Vaughan. *6–8*. Parts of the same equatorial section showing embryonic and equatorial chambers, *6*, *7*, ×40; *8*, ×20. *9–10*. Two different enlargements of the same vertical section made from the specimen illustrated by *6–8*; *9*, ×40; *10*, ×20; loc. 6019g. (p. 333)
11, *12*—*Lepidocyclina* (*Lepidocyclina*) *parvula* Cushman. Vertical sections of the same specimen, *11*, ×20; *12*, ×40; loc. 6257. (p. 335)
13, *14*—*Lepidocyclina* (*Lepidocyclina*) *waylandvaughani* Cole. Two different enlargements of the same vertical section, *13*, ×40; *14*, ×20; loc. 6019a. (p. 336)

A. Test stellate ..... *L. asterodisca*
B. Test not stellate:
1. Surface of the test with umbonal papillae and radiating costae ..... *L. giraudi*
2. Surface of the test without costae, either with or without papillae:
a. Equatorial chambers rhombic or diamond-shaped:
1′. Vertical sections without pillars or with fine pillars ..... *L. yurnagunensis*
2′. Vertical sections with strong pillars ..... *L. yurnagunensis morganopsis*
b. Equatorial chambers near periphery spatulate to elongate hexagonal:
1′. Vertical sections with strong, irregularly distributed pillars ... *L. parvula*[1]
2′. Vertical sections without pillars, or with small or moderate pillars:
a′. Lateral chambers in definite, regular tiers with open cavities:
1″. Lateral chambers long
a‴. With abundant, strong pillars ..... *L. sanluisensis*
b‴. With irregularly distributed fine or moderate pillars ..... *L. miraflorensis*
2″. Lateral chambers short
a‴. With or without weak pillars ..... *L. canellei*[2]
b′. Lateral chambers not in definite tiers:
1″. Cavities of lateral chambers low, appressed, between floors and roofs which are thicker than the height of the cavity:
a‴. Cavities long, slit-like ..... *L. mantelli*
b‴. Cavities low, slightly arched, but with a distinct opening ..... *L. supera*[3]
2″. Cavities of lateral chambers with greater height than the thickness of the floors and roofs:
a‴. Cavities long ..... *L. californica*
b‴. Cavities short ..... *L. waylandvaughani*

[1] *L. colei* Gravell and Hanna is probably a synonym of *L. parvula*.
[2] *L. matleyi* Vaughan is probably a synonym of *L. canellei*.
[3] *L. forresti* Vaughan is a synonym of *L. supera*.

larger than those near the rim. The larger centrally located papillae have diameters of 80 to 100μ, whereas the smaller papillae near the rim have diameters of about 40μ. The individual papillae have radiating from them fine, white lines that outline the rather large lateral chambers. The rim, which is normally devoid of lateral chambers, shows the outlines of the radially elongate, hexagonal equatorial chambers. The outer edge of the rim is not inflated, although in some specimens there is a gradual, but slight thickening of the rim toward the periphery.

The embryonic chambers are bilocular and subequal. The dividing partition between the chambers is straight. The outer wall of the embryonic chambers is thick.

Detailed measurements of equatorial and vertical sections are given on page 335.

The equatorial chambers are elongate hexagonal when fully developed. However, certain chambers are short spatulate and others are arcuate. There is normally an increase in the length of the radial diameter of the chambers as they approach the periphery of the test, but other chambers do not show this increase.

The lateral chambers, which have very thin floors and roofs, are large, open, and rectangular and are arranged in regular tiers. Small pillars occur unequally distributed through the vertical sections, with the largest and most numerous pillars appearing over the embryonic chambers.

Remarks.—Only a single specimen of *L. miraflorensis* was present in the sample from loc. 5866. This specimen was ground to an equatorial section and photographed. Then a half vertical section was made of this specimen and this half section in turn was photographed.

The two specimens available from loc. 6019f represent natural equatorial sections of microspheric individuals. Cushman's illustrations (1918, pl. 35, fig. 3 and pl. 36) are good. These specimens probably represent the microspheric generation of *L. miraflorensis*.

In the rock from loc. 6019g two specimens

MEASUREMENTS OF EQUATORIAL SECTIONS OF *LEPIDOCYCLINA MIRAFLORENSIS*

Locality	Topotype specimens USGS loc. 6255			5866
Diameter	5.+mm.	6.+mm.	4.6+mm.	4.2+mm.
Embryonic chambers:				
Diameters of initial chamber	200×340μ	220×360μ	160×260μ	170×340μ
Diameters of second chamber	200×360μ	180×395μ	150×290μ	200×375μ
Distance across both chambers	420μ	420μ	320μ	390μ
Thickness of outer wall	35μ	40μ	40μ	40μ
Equatorial chambers:				
Near center:				
Radial diameter	80–100μ	100–120μ	100–120μ	—
Tangential diameter	60–80μ	60–80μ	85μ	—
Near periphery:				
Radial diameter	60μ	60μ	40–60μ	80μ
Tangential diameter	40μ	40–60μ	60μ	40μ

were found. One was a natural equatorial section of a small microspheric individual with a diameter of about 6 mm. The equatorial chambers are the same shape as those of the specimens from loc. 6019f. It was possible, however, to grind a half vertical section of the specimen from loc. 6019f. The lateral chambers are the same type as those found in the megalospheric generation of *L. miraflorensis*.

The second specimen from locality 6019g is a small megalospheric individual exposed on the ground surface of the matrix material. The observable features indicate that it is *L. miraflorensis*.

LEPIDOCYCLINA (LEPIDOCYCLINA) PARVULA Cushman

Plate 44, figures 11, 12

1918. *Lepidocyclina parvula* CUSHMAN, Carnegie Inst. Washington Publ. 291, p. 58, pl. 3, figs. 4–7.

1952. *Lepidocyclina* (*Lepidocyclina*) *parvula* Cushman. COLE, U. S. Geol. Survey Prof. Paper 244, p. 20, pl. 15, figs. 6–10.

Diameter, about 3 mm.; thickness

MEASUREMENTS OF VERTICAL SECTIONS OF *LEPIDOCYCLINA MIRAFLORENSIS*

Locality	Topotype specimens USGS loc. 6255			5866
Diameter	6.2+mm.	5.8+mm.	4.5+mm.	4.2+mm.
Thickness	1.0mm.	0.92mm.	0.76mm.	0.52mm.
Diameter of umbo	2.4mm.	3.0mm.	3.2mm.	2.0mm.
Width of flange	2.0mm.	1.6mm.	—	1.4mm.
Thickness of flange at periphery	0.22mm.	0.24mm.	—	—
Embryonic chambers:				
Length	340μ	420μ	340μ	360μ
Height	340μ	340μ	280μ	200μ
Thickness of outer wall	35μ	20μ	40μ	40μ
Lateral chambers:				
Number to a tier at each side of embryonic chamber	10	9	8	4
Length	140–220μ	160μ	80–100μ	80μ
Height	20μ	20μ	20μ	20μ
Thickness of floors and roofs	5μ	5μ	5μ	5μ
Surface diameter of pillars	80μ	80μ	40–100μ	20–40μ

through the center, about 0.9 mm.; shape biconvex, with a group of large, umbonal pustules.

The embryonic chambers are bilocular, with a thick outer wall. These chambers have internal diameters of 240 and 260μ.

The equatorial chambers are spatulate to hexagonal. Peripheral equatorial chambers have tangential diameters of about 50μ and radial diameters of about 70μ. The equatorial chambers have a height of about 80μ at the center of the test and 160μ at the periphery, these measurements including the thickness of the floors and roofs.

The lateral chambers overlap from one tier to the adjacent one. They have rather thick roofs and floors, about 10 to 20μ. The cavities of the outer chambers have a length of about 120μ and a height of about 30μ. There are about six lateral chambers to a tier on each side of the embryonic chambers.

Strong pillars with a surface diameter of 160 to 200μ are irregularly scattered through the central area of the test.

Remarks.—A single microspheric specimen was recovered from the sample collected at locality 6257. Although badly chipped, this specimen shows surface costae of the type developed by microspheric specimens of *L.* (*L.*) *giraudi* R. Douvillé (1907, p. 307). At first, this specimen was identified as that species, but the discovery of the megalospheric specimen, identified as *L.* (*L.*) *parvula*, indicates that this microspheric specimen should be classified with that species. It probably represents one of the races of *L. parvula* similar to the type named *L. parvula crassicosta* Vaughan and Cole (in Vaughan, 1933, p. 17).

Lepidocyclina (Lepidocyclina) waylandvaughani Cole
Plate 44, figures 13, 14

1918. *Lepidocyclina canellei* Cushman, *not* Lemoine and Douvillé 1904, U. S. Nat. Mus. Bull. 103, pp. 91, 92 (part), pl. 34, figs. 2, 3a, b.
1928. *Lepidocyclina* (*Lepidocyclina*) *waylandvaughani* Cole, Bull. Amer. Paleont., vol. 14, no. 53, pp. 21, 22, pl. 4, figs. 1–8.
1952. *Lepidocyclina* (*Lepidocyclina*) *waylandvaughani* Cole. Cole, U. S. Geol. Survey Prof. Paper 244, pp. 20–22, pl. 18, figs. 1–10, 16, 17.

Cushman (1918, pl. 34, figs. 2, 3a, b) figured three accidental equatorial sections of *L.* (*L.*) *waylandvaughani*, but he identified them as *L.* (*L.*) *canellei* Lemoine and R. Douvillé (1904, p. 20). Although his illustrations show the bilocular embryonic apparatus and hexagonal equatorial chambers that characterize both *L. waylandvaughani* and *L. canellei*, he did not illustrate a vertical section that is the critical one. However, in the same material from loc. 6019a, a specimen was found from which a vertical section was cut. This vertical section proves that these specimens are *L. waylandvaughani*, not *L. canellei*.

The vertical section is very slightly oblique. The measurements of this section follow: length, 4.4+ mm.; thickness at center, 0.9+ mm.; embryonic chambers: height 250μ, length 340μ, thickness of outer wall 40μ; height of equatorial layer—including floor and roof thickness—at the center 80μ, at the periphery 200μ; lateral chambers: number at center on each side of the embryonic chambers 8, height 30μ, length 140μ, thickness of floors and roofs 20μ; surface diameter of pillars 120μ.

The lateral chambers overlap. The roofs and floors are very slightly curved, and the chamber cavities are distinct, open.

Remarks.—The vertical section (pl. 44, fig. 13) has a strong pillar of the type which characterizes *L. waylandvaughani* developed on the right side above the embryonic chambers. The lateral chambers are not in definite tiers. The floors and roofs of the lateral chambers are moderately thick, and slightly curved. These are characteristics of *L. waylandvaughani* rather than *L. canellei*.

Miogypsina (Miolepidocyclina) panamensis (Cushman)
Plate 44, figures 1–5

1918. *Heterosteginoides panamensis* Cushman, U. S. Nat. Mus. Bull. 103, p. 97, pl. 43, figs. 3–8 (not figs. 1, 2, which are *Miogypsina antillea*).
1952. *Miogypsina* (*Miolepidocyclina*) *panamensis* (Cushman). Cole, U. S. Geol. Survey Prof. Paper 244, pp. 36, 37, pl. 25, figs. 1–8.
1952. *Miogypsina panamensis* (Cushman). Drooger, Doctor's Diss. Utrecht, pp. 17–19, 48, 49, pl. 1, figs. 11–15.
1952. *Miogypsina ecuadorensis* Tan. Drooger, Doctor's Diss. Utrecht, pp. 19, 20, 48, 49, pl. 1, figs. 25–29.

Numerous accidental sections of specimens assigned to this species occur at loc. 6257. Although an oriented equatorial section was not seen, the oblique "equatorial" sections and the vertical sections show definitely that the embryonic chambers are located in a subcentral position and are partially surrounded by a coil of quadrate chambers before the normal equatorial chambers develop.

Drooger (1952, p. 48) considered that *M. ecuadorensis* is a distinct species and should not be included in the species *M. panamensis*. However, the differences between these species are so slight that it is doubtful if this position can be maintained. Although Drooger stated "in *M. ecuadorensis* the intercalary chambers and the chambers of the deuteroconchal spire from the first principal auxiliary chamber are more numerously developed than in *M. panamensis*," it can be proven that slight variation of this type is the result either of individual variation within members of a single population from a given locality or geographic variation. It is not necessarily an evolutionary development as Drooger (1952, fig. 17) implies. Myers (1942, p. 333) has demonstrated in certain living Foraminifera that "the rate of growth in numbers of chambers was about 40 per cent more and the diameters of the tests 60 per cent larger in *E. crispum* living in the sublittoral zone than in those from the littoral zone." Many other examples of this type of variation could be given.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 338–346, PLS. 45, 46, 1 TEXT FIG., MAY 1953

POLYMORPHINIDAE OF THE CRETACEOUS (CENOMANIAN) DEL RIO SHALE

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ABSTRACT—Nineteen species of the Polymorphinidae, six of which are new, are described and illustrated from the Del Rio (Cenomanian) Cretaceous shale of central Texas. The abundance of specimens and the variety of forms including attached specimens indicates that the Polymorphinidae attained a high stage of development long before the Tertiary. Two new species are described under the genus *Enantiomarginulina*, recorded for the first time from an American fauna.

INTRODUCTION

THE oldest representatives of the family Polymorphinidae occur in the Triassic (Cushman and Ozawa, 1930, pp. 1–7; Cushman, 1948, p. 221). Gradual and unimpressive evolution within the family has previously been recognized as developing during the Jurassic, Lower Cretaceous, and Upper Cretaceous. Most workers have agreed that the greatest expansion in kinds and numbers of polymorphinids occurred at the beginning of the Tertiary (Cushman, 1948, p. 222; Galloway, 1933, p. 255), and early Tertiary genera continue with only a few exceptions to the Recent.

An analysis of foraminiferal suites from the Del Rio shale at Austin, Texas, indicates that previously accepted generalities about the polymorphinids should be challenged. The 19 species distributed among eight genera of Polymorphinidae herein described and illustrated are evidence that a notable evolution of the family took place at least as early as Cenomanian time. Further, all of the various modes of growth known to the family, such as free, attached, fistulose, tubulose, and racemose, are represented in the Del Rio fauna. This evidence suggests that the family had reached a mature stage in its development long before the Tertiary. The presence of numerous specimens of sessile species indicates that this mode of growth is not so rare as has been assumed (Tappan, 1943, p. 505, and others).

ACKNOWLEDGMENTS

The material in this paper represents a portion of a study completed as a master's thesis at The University of Texas (Bullard, 1951). Very grateful acknowledgments are made to Dr. Samuel P. Ellison, Jr., who supervised the thesis work and aided in drafting and photographing the illustrations, and to Dr. Fred M. Bullard, who assisted in collecting the samples and contributed invaluable aid in the details of the photomicrography.

LOCALITIES AND LITHOLOGIES

The specimens described here were obtained from localities in Austin, Travis County, Texas where the Del Rio is estimated to be 80 feet thick. Its main components are bedded calcareous clays and claystones with local sandstone lenses and thin limestones. The clays and claystones contain gypsum, pyrite, ferruginous nodules, and bentonitic layers. Tentative detailed correlation of sections is based on megafossils: *Exogyra arietina* Roemer and *Kingena wacoensis* (Roemer) are abundant in the lower part of the Del Rio, and *Gryphaea graysonana* Stanton is common in the upper part. Large numbers of *Exogyra arietina* occur in distinct beds which are locally valuable as correlation markers.

Since no single exposure shows the entire Del Rio section in the Austin area, three sections, A, B, and C (figure 1), were combined as the most representative. From paleontological evidence it is believed that they do not overlap appreciably, although a few feet at the base of section C may correlate with the uppermost levels of the basal section B.

Section B is located on the west bank of Shoal Creek at 19th Street where 18 feet of gray-brown, slightly greenish, poorly bedded, soft clays of the Del Rio are exposed in contact with light gray, hard, rather massive Georgetown limestone. Forty feet of Del Rio are exposed by faulting at location C on the west bank of Shoal Creek near 32nd Street. This middle section consists of finely bedded, dense, massive shales and clays ranging from greenish-gray to yellowish in color, with ferruginous laminae and selenite bands. The exact stratigraphic level of this part of the section is uncertain, but field evidence and paleontological data indicate that this exposure does not contain the upper contact of the formation as previously reported (Plummer, 1931, p. 122, and others). This locality is that described as "Del Rio, Shoal Creek, Austin" by Carsey, 1926, and as Bureau of Economic Geology Station 226-T-10 by Plummer, 1931, and it is the type locality for several of the more closely restricted Del Rio Foraminifera: *Textularia washitensis* Carsey, *T. rioensis* Carsey, *Gaudryinella delrioensis* Plummer, *Valvulineria asterigerinoides* Plummer, *Globorotalia delrioensis* Plummer. *Exogyra arietina* is very abundant in this section below sample 15. The microfauna is unusually prolific. The top of the Del Rio is exposed at locality A, Barton Springs Road and Lamar Boulevard, where it is in contact with the Buda limestone. The contact is transitional, with the upper 2 to 3 feet of the Del Rio consisting of a section of greenish-white, poorly bedded marls with secondary carbonate deposits in the form of calcareous nodules. Eighteen feet of section below the transition zone consist of light gray to brownish, massive to thinly bedded, compact shales with abundant selenite crystals. The microfauna is prolific and varied, and the distinctive agglutinated foraminifer *Haplostiche texana* occurs only at this locality and level.

TYPES

All figured and listed specimens, including syntypes, topotypes, and hypotypes, are deposited in The University of Texas Micropaleontological Collections and bear accession numbers of that collection.

GENERAL SIGNIFICANCE OF THE POLYMORPHINID FAUNA

The extensive development of the Polymorphinidae by Del Rio time reflects a rapid expansion of the family during the Washita; in comparison with eight species from the Duck Creek, basal Washita (Tappan, 1943), and 10 species from the Grayson (Tappan, 1940), 19 polymorphinids are recorded from the Del Rio. Stanton (1947, p. 2) doubts that the Grayson and the Del Rio are exact time equivalents, although they appear to be synchronous at their bases; and the diversity of their polymorphinid faunas supports his thesis.

The value of these species as guide fossils has not yet been determined.

ECOLOGY

The characteristic ecology of the family is that of a neritic environment of relatively warm shallow waters. The Del Rio Polymorphinidae are somewhat more abundant in samples from the middle marly shales and clays than from levels near the upper and lower contacts.

ATTACHED FORMS

Del Rio sessile polymorphinids are most commonly attached to *Exogyra arietina* shell fragments but are also found adhering to echinoid plates and *Inoceramus* prisms. This habit suggests that their stratigraphic occurrence is directly related to the occurrence of *Exogyra*, which is limited to the lower portion of the Del Rio section. It is difficult to determine the phylogenetic significance of the attached forms, since relatively few have been recorded. Some evidence, however, is found in this Del Rio assemblage: it contains an unattached form comparable to each attached species from which the attached form may have developed. One interpretation of this observation might be that in a period of ecologic change, such as a muddying of the waters or an intensification of currents, certain species were able to develop attachment plates and become fixed, thus improving their chance of survival. The kind of attachment found among these polymorphinids probably augmented the efficiency of the terminal aperture, which is mostly enveloped by the attach-

ment chamber with its irregularly branching tubes. These tubes terminate in several rounded openings, some having slight necks. The whole attachment is surrounded by a thin transparent keel. Parasitism has been mentioned with regard to the attached polymorphinids (Cushman and Ozawa, 1930, p. 139), but evidence is lacking in support of it. The fact that they are found clinging to both inner and outer sides of the shells to which they adhere would possibly indicate the contrary. It is doubtful, also, that these attached forms represent degenerate species, since in other respects they so closely resemble species having greater stratigraphic ranges throughout the section and since they occur in profusion in certain samples. It seems probable that they may represent a specialized adaptation to an ecological niche provided by the prevalence of available firm attachment bases, such as *Exogyra arietina* shells.

CLASSIFICATION

Classification of fossil forms must essentially be morphological in nature, but it best serves its purpose if phylogenetic relationships can be reflected in its scheme. If morphological continuities can be established, it is, therefore, necessary that they be followed in systematizing the forms. Also, it should be realized that classification is set up as an aid to workers in paleontology, and it is best suited to this purpose with a minimum of categories to be handled. With these considerations in mind, the author has referred the present attached species to genera which are established on the basis of chamber arrangement of the earlier stages; and these are clearly evident. Morphology suggests that the attached forms were derived from the similar unattached species found in the same environment. Therefore, it is logical and most practical to refer them to the same genera. The numbers of attached specimens found here indicate that this mode of growth had some ecological and genetic significance and was not merely the result of individual aberration.

Some specimens are referred to Marie's *Enantiomarginulina* and placed with the Polymorphinidae under the subfamily Enantiomorphininae with some question until further work determines their exact relationships. They appear to be transitional forms between *Marginulina* and the Polymorphinidae.

DESCRIPTION OF FORAMINIFERA

Family POLYMORPHINIDAE

Subfamily ENANTIOMORPHININAE

Genus ENANTIOMARGINULINA Marie, 1941

ENANTIOMARGINULINA SIMILIS Bullard, n. sp.

Plate 45, figures 1–4

Test medium in size, elongate, cylindrical, nearly rounded in section; early chambers arranged in a spiral series, rapidly uncoiling, initial coil produced to form an elongate hook; later chambers becoming uniserial, alternating, rapidly inflating as added; surface smooth, margins lobulate, dorsal margin convex; sutures depressed, straight or slightly curved, oblique; aperture radiate at the dorsal angle. Lengths of figured specimens vary from .28 mm. to .4 mm.; widths, from .1 mm. to .18 mm.

Types.—Syntypes from sample 16, location C; U.T. 1036.

This species is quite variable in amount of inflation of the chambers and in degree of

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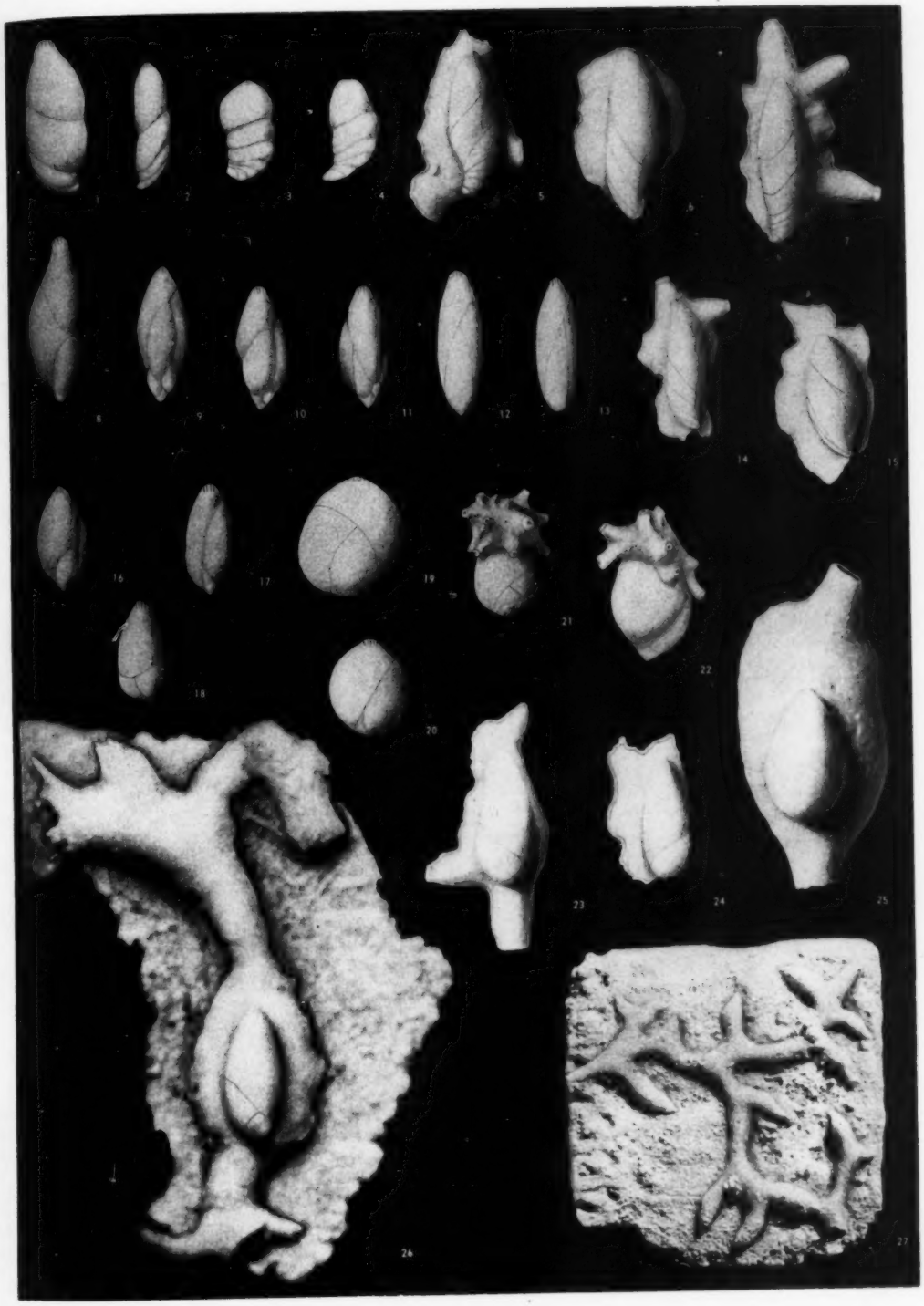
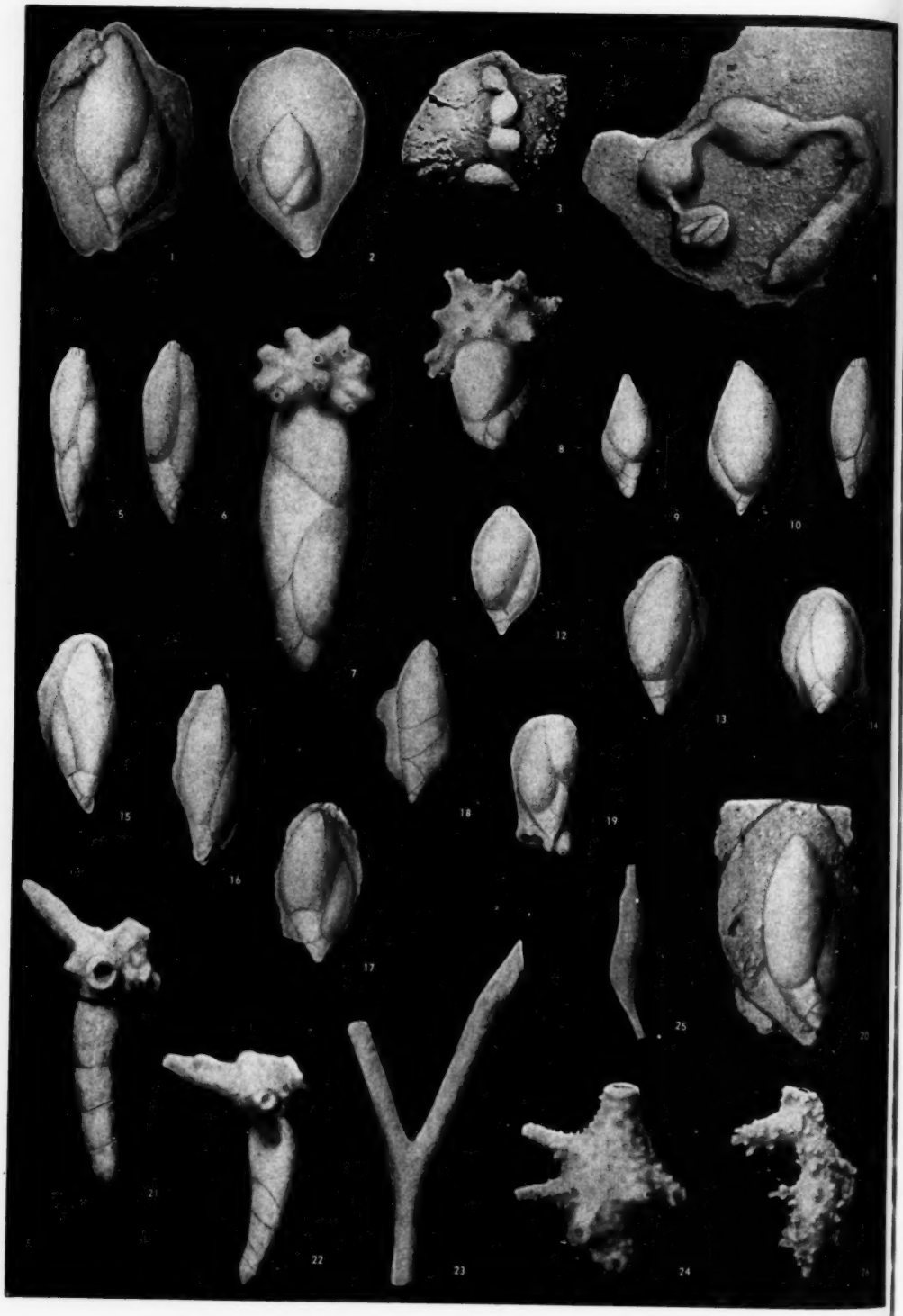
EXPLANATION OF PLATE 45

(All figures ×50 unless otherwise indicated)

FIGS. *1–4—Enantiomarginulina similis* Bullard, n. sp. Syntypes, U.T. 1036. (p. 340)
5–7, 14, 15—Enantiomarginulina enigmata Bullard, n. sp. Syntypes, U.T. 1090. (p. 341)
8—Eoguttulina anglica Cushman and Ozawa. (p. 341)
9–11—Paleopolymorphina ozawai Tappan. (p. 341)
12, 13—Guttulina exepolita Bullard, n. sp. Syntypes, U.T. 1077. (p. 341)
16—18—Globulina exserta (Berthelin). (p. 342)
19, 20—Globulina lacrima Reuss. (p. 342)
21, 22—Globulina fistulosa Bullard, n. sp. Syntypes, U.T. 1080. (p. 342)
23–27—Globulina cervicornis (Chapman). *23–25*, ×50, attached tubular growths broken. *26*, attached to *Inoceramus* prism. *27*, ×15, globuline portion broken from specimen, tubular growths attached to echinoid plate. (p. 342)



Bullard, Texas Cretaceous Polymorphinidae



Bullard, Texas Cretaceous Polymorphinidae

initial coiling. It is distinct from various *Marginulina* species in having the initial spiral series and the alternating uniserial chamber arrangements. It is rare in the Del Rio.

No American specimens have been referred to this genus, which was described by Marie from the Chalk of the Paris Basin (Marie, 1941). It was erected under the new family Enantiomorphinidae in this work and has since been recorded as such by H. Thalmann in his *Index* (1947) and by Payard (1947, p. 175) (personal communication, Dr. Brooks F. Ellis). The whole group is probably transitional between the Lagenidae and the Polymorphinidae. The Del Rio specimens are placed in the latter family until further work establishes more definite evidence of their relationships.

ENANTIOMARGINULINA ENIGMATA
Bullard, n. sp.
Plate 45, figures 5–7, 14, 15

Test initially free, later attached; enantiomarginuline portion small to medium in size, elongate; chambers initially slightly coiled, later in an alternating uniserial arrangement, not much inflated, nearly even in height; test embedded in attachment plate, acuminate toward both extremities, wall smooth; attachment plate irregular, with a thin hyaline keel, developing short stout tubes at the ends of which are located rounded apertures. Lengths of figured specimens vary from .325 mm. to .475 mm.; widths, from .113 mm. to .13 mm.

Types.—Syntypes from sample 16, location C; U.T. 1090.

This species is rare in the Del Rio, being found only in samples 16 and 17. It differs from *E. similis* in being attached and in having less inflated chambers which are nearly equal in size.

Subfamily POLYMORPHININAE
Genus EOGUTTULINA Cushman & Ozawa, 1930
EOGUTTULINA ANGLICA Cushman & Ozawa
Plate 45, figure 8

Eoguttulina anglica CUSHMAN & OZAWA, 1930, U. S. Nat. Mus., Proc., vol. 77, art. 6, p. 16, pl. 1, figs. 3a–c.

The Del Rio form appears identical with the figure given by Cushman and Ozawa, which was described from the Cambridge Greensands. It is rare here, occurring only in the lower section at C, sample 16.

Type.—Hypotype, U.T. 1076.

Genus PALEOPOLYMORPHINA Cushman & Ozawa, 1930
PALEOPOLYMORPHINA OZAWAI Tappan
Plate 45, figures 9–11

Paleopolymorphina ozawai TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 113, pl. 17, figs. 20a–21c. ——, 1943, idem, vol. 17, p. 504, pl. 80, fig. 35.

This species is common in the marly section of the Del Rio at location C. It ranges throughout the Washita and is found in the Del Rio at all levels except the lower ones.

Types.—Hypotypes, U.T. 1075.

Genus GUTTULINA D'Orbigny, 1839
GUTTULINA EXEPOLITA Bullard, n. sp.
Plate 45, figures 12, 13

Test slender, elongate, cylindrical; chambers overlapping, extending to the base of the test; initial chamber may have a short

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EXPLANATION OF PLATE 46
(All figures ×50)

FIGS. *1, 2*—*Globulina immobilis* Bullard, n. sp. Syntypes, U.T. 1084. (p. 343)
3, 4—*Globulina laevis* (Sollas). *3*, attached to *Exogyra arietina* fragment. *4*, showing early globuline stage, last chamber distorted; attached to *Exogyra arietina* fragment. (p. 343)
5, 6—*Pyrulina cylindroides* Roemer. (p. 343)
7, 8—*Pyrulina longa* Tappan. *8*, megalospheric form. (p. 344)
9–12—*Pyrulina shoalcreekensis* Bullard, n. sp. Syntypes, U.T. 1087. (p. 344)
13–20—*Pyrulina brykerwoodensis* Bullard, n. sp. Syntypes, U.T. 1088, 1089. *18*, laterally attached specimen. (p. 344)
21, 22—*Pseudopolymorphina roanokensis* Tappan. (p. 344)
23—*Ramulina abscissa* Loeblich and Tappan. (p. 344)
24, 25—*Ramulina globulifera* Brady. (p. 346)
26—*Ramulina novaculeata*, Bullard, n. name. (p. 346)

basal spine; sutures slightly depressed, indistinct; margins smooth; aperture terminal, radiate.

This form is distinctive for its smooth cylindrical shape. It is common at several levels in the middle section of the Del Rio. Lengths vary slightly from .4 mm., widths, .125 mm.

Types.—Syntypes from locality C, sample 16; U.T. 1077.

Genus GLOBULINA D'Orbigny, 1839
GLOBULINA EXSERTA (Berthelin)
Plate 45, figures 16–18

Polymorphina exserta BERTHELIN, 1886, Soc. géol. France, Mém., sér. 3, t. 1, p. 51, pl. 4, figs. 22a–23b.
Polymorphina buccalenta BERTHELIN, 1880, idem, p. 58, pl. 4, figs. 16a–17b.
Globulina exserta CUSHMAN & OZAWA, 1930, U. S. Nat. Mus., Proc., vol. 77, art. 6, p. 78, pl. 19, figs. 5–7.——TAPPAN, 1943, Jour. Paleontology, vol. 17, p. 504, pl. 80, figs. 36, 37.

This species differs from *G. lacrima* in being more elongate, having a produced initial extremity, and possessing depressed sutures. It has been recorded as common in the Cretaceous of Europe and has been found in the Fredricksburg and lower Washita groups in this country. The range is here extended through the Washita to include the Del Rio, where the species is common.

Types.—Hypotypes, U.T. 1078.

GLOBULINA LACRIMA Reuss
Plate 45, figures 19, 20

Polymorphina (*Globulina*) *lacrima* REUSS, 1845, Verstein. böhm. Kreide-formation, pt. 1, p. 40, pl. 12, fig. 6; pl. 13, fig. 83.—— EGGER, 1899, K. bayer. Akad. Wiss., Math.-naturh. Abt., Abh., Cl. 2, vol. 21, pt. 1, p. 125, pl. 17, figs. 39, 40.
Globulina lacrima REUSS, 1851, Haidinger's Nat. Abh., vol. 4, p. 27, pl. 4, fig. 9.—— CUSHMAN and OZAWA, 1930, U. S. Nat. Mus., Proc., vol. 77, art. 6, pl. 19, figs. 1, 2.—— CUSHMAN, 1931, Tenn. Div. Geology Bull. 41, p. 40, pl. 6, figs. 9a–c;—— 1932, Jour. Paleontology, vol. 6, p. 337, pl. 51, fig. 2;—— 1936, Bull. Geol. Soc. America, vol. 47, p. 418.—— LOETTERLE, 1937, Nebraska Geol. Survey Bull., 2d ser., Bull. 12, p. 31, pl. 4, figs. 4a, b.—— FRIZZELL, 1943, Jour. Paleontology, vol. 17, p. 348, pl. 56, fig. 27.——CUSHMAN & TODD, 1943, Cushman Lab. Foram. Research, Contr., vol. 19, p. 61, pl. 11, fig. 3.—— CUSHMAN, 1944, idem, vol. 20, p. 9, pl. 2, fig. 10;—— 1944, idem, p. 89, pl. 13, fig. 28;—— 1944a, Am. Jour. Science, vol. 242, p. 612, pl. 2, fig. 10;—— 1946, U. S. Geol. Survey Prof. Paper 206, p. 96, pl. 40, figs. 11, 12.
Polymorphina gibba CUSHMAN (not D'Orbigny), 1926, Bull. Am. Assoc. Petr. Geol., vol. 10, p. 604, pl. 20, figs. 8, 15.

Globulina lacrima is widely recorded from the Cretaceous of Europe and America, although most of the records are from Upper Cretaceous strata. This is the first note of it from the Washita, where it occurs sparingly throughout the section.

Types.—Hypotypes, U.T. 1079.

GLOBULINA FISTULOSA Bullard, n. sp.
Plate 45, figures 21, 22

Globulina lacrima var. *subspherica*, CUSHMAN & OZAWA (not Berthelin), 1930, U. S. Nat. Mus., Proc., vol. 77, art. 6, p. 78, pl. 19, fig. 6 (not figs. 5 and 7).—— TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 113, pl. 17, figs. 24a, b.

Test small, oval in outline, base slightly pointed; chambers few, inflated, extending nearly back to base of test; sutures faintly depressed; wall smooth; apertural end fistulose, with numerous openings at the ends of short tubes. Lengths vary from .375 mm. to .475 mm.; widths, from .275 mm. to .375 mm.

This form differs from *G. lacrima* in possessing the fistulose growth and in being slightly more compressed with a bluntly pointed initial extremity. It differs from Berthelin's *Polymorphina subspherica* in having the fistulose growth and in lacking the broadly rounded base. It is distinct from Reuss' *Globulina lacrima* var. *horrida* in lacking the finely spinose surface. *G. fistulosa* should not be confused with megalospheric forms of *Pyrulina longa*, which are more compressed and cylindrical in outline and have a more pointed base. The species is rare in the Del Rio, although Tappan found it common in the Grayson. It was not recognized in the lower levels at locality B.

Types.—Syntypes from location C, sample 16; U.T. 1080.

GLOBULINA CERVICORNIS (Chapman)
Plate 45, figures 23–27

Polymorphina orbignyi Zborzewski var. *cervicornis* CHAPMAN, 1892, Geol. Mag., n. ser., dec. 3, vol. 9, p. 54, pl. 2, figs. 5, 6.
Ramulina cervicornis CHAPMAN, 1896, Royal Micr. Soc., Jour., p. 584, pl. 12, figs. 10, 11.
Vitriwebbina cervicornis EICHENBERG, 1934, Niedersächs geol. Vereins zu Hannover Jahresb. 26, p. 184, pl. 16, fig. 2

Bullopora cervicornis TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 114, pl. 18, fig. 5. ——, 1943, idem, vol. 17, p. 507, pl. 81, fig. 10.
Bullopora sp. TAPPAN, 1940, op. cit., p. 114, pl. 18, fig. 7.
Globulina redriverensis TAPPAN, 1943, Jour. Paleontology, vol. 17, p. 505, pl. 81, figs. 1a–3.
Bullopora irregularis LOZO, 1944, Am. Midland Nat., vol. 31, p. 559, pl. 1, fig. 9.
Histopomphus cervicornis, LOEBLICH & TAPPAN, 1949, Jour. Paleontology, vol. 23, p. 263, pl. 50, fig. 10.

Chapman described this species as having an initial "polymorphine arrangement of chambers, which proceeds to take on a wild flattened fistulose growth . . . "; as Loeblich and Tappan have recognized (1949, p. 262), many incomplete specimens or forms from which the globuline portion has been broken have been referred to *Bullopora* and *Vitriwebbina*. Since the early chambers are arranged in the manner of *Globulina*, the species is referred to that genus. Loeblich and Tappan's *Histopomphus redriverensis* (Tappan), which has "a stouter polymorphine portion, and a more rapidly branching attached portion" (1949, p. 263), is considered the same as Chapman's original species, since the very irregular character of the branching tubes and the variation in inflation of the earlier chambers preclude such distinctions among the Del Rio specimens.

Types.—Hypotypes from samples 13, 16 and 17, location C; U.T. 1081, 1082, 1083.

GLOBULINA IMMOBILIS Bullard, n. sp.
Plate 46, figures 1, 2

Initial chambers globuline, test oval to rounded in outline, initial extremity slightly produced; chambers few, slightly inflated; wall smooth; sutures depressed or indistinct; test later attached by a rounded or slightly irregular attachment plate extending from the terminal aperture; wall of attachment plate smooth, periphery with a thin transparent keel; aperture single, rounded, at the end of a small protuberance of the attachment plate, with a slight hyaline neck. Lengths vary from .575 mm. to .625 mm.; widths, from .4 mm. to .425 mm.

Types.—Syntypes from sample 16, location C; U.T. 1084.

This species differs from *G. cervicornis* in possessing a less inflated globuline portion which has a produced initial extremity, in having a smooth rounded attachment plate without the irregular tubular growths, and in having the single aperture. It is rarer than *G. cervicornis*.

GLOBULINA LAEVIS (Sollas)
Plate 46, figures 3, 4

Webbina laevis SOLLAS, 1877, Geol. Mag., dec. 2, vol. 4, p. 103, pl. 6, figs. 1–3.
Vitriwebbina laevis CHAPMAN, 1892, idem, dec. 3, vol. 8, p. 53, pl. 2, fig. 4;—— 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 18, p. 332, text fig. 3;——1896, Roy. Micr. Soc. Jour., p. 585, pl. 12, fig. 12.—— BAGG, 1898, U. S. Geol. Survey Bull. 88, p. 36, pl. 2, figs. 4a, b.——CHAPMAN, 1899, Ann. Mag. Nat. Hist., ser. 7, vol. 3, p. 314.—— WELLER, 1907, New Jersey Geol. Survey, Paleontology, vol. 4, p. 205, pl. 1, figs. 40, 41.—— CHAPMAN, 1917, Western Australia Geol. Survey Bull. 72, p. 37, pl. 11, fig. 101.
Bullopora laevis WICKENDEN, 1932, Jour. Paleontology, vol. 6, p. 206, pl. 29, figs. 6–8.—— CUSHMAN, 1933, Cushman Lab. Foram. Res., Spec. Publ. 5, pl. 22, figs. 24.—TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 115, pl. 18, fig. 6;—— 1943, idem, vol. 17, p. 507, pl. 81, figs. 11, 12.—— CUSHMAN & TODD, 1943, Cushman Lab. Foram. Res., Contr., vol. 19, p. 63, pl. 11, fig. 8.——LOZO, 1944, Am. Midland Nat., vol. 31, p. 560, pl. 3, fig. 2.—— CUSHMAN, 1944, Cushman Lab. Foram. Res., Contr., vol. 20, p. 9, pl. 2, fig. 33;—— 1946, U. S. Geol. Survey Prof. Paper 206, p. 98, pl. 42, figs. 1–4—— STEAD, 1951, Texas Jour. Sci., p. 596, pl. 3, figs. 14, 15.

This is a well known species which has a distinct *Globulina* initial stage, followed by additional attached chambers varying in shape and connected by short tubes. It differs from *Globulina immobilis* in having the numerous attached chambers and a smaller globuline stage. It is rare in the Del Rio.

Types.—Hypotypes, samples 16, 17, location C; U.T. 1095.

Genus PYRULINA D'Orbigny, 1839

PYRULINA CYLINDROIDES (Roemer)
Plate 46, figures 5, 6

Polymorphina cylindroides ROEMER, 1838, Neues Jahrb., p. 385, pl. 3, fig. 26.——BRADY, PARKER, & JONES, 1870, Trans. Linnean Soc., vol. 27, p. 221, pl. 39, figs. 6a–c.
Polymorphina fusiformis CUSHMAN (not Roemer), 1926, Am. Assoc. Petr. Geol. Bull., vol. 10, p. 604, pl. 20, fig. 14.
Polymorphina gutta BERRY & KELLEY (not D'Orbigny), 1929, U. S. Nat. Mus., Proc., vol. 76, art. 19, p. 10, pl. 1, fig. 11.
Pyrulina cylindroides CUSHMAN & OZAWA, 1930, idem, vol. 77, art. 6, p. 56, pl. 14, figs. 1–5.—— CUSHMAN, 1931, Tenn. Div. Geol. Bull. 41,

p. 40, pl. 6, figs. 7, 8;—— 1933, Cushman Lab. Foram. Res., Spec. Publ. 5, pl. 22, fig. 14.—— TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 114, pl. 18, figs. 1a–c.—— CUSHMAN & TODD, 1943, Cushman Lab. Foram. Res., Contr., vol. 19, p. 62, pl. 11, fig. 2.——CUSHMAN, 1944, idem, vol. 20, p. 9, pl. 2, fig. 16.—— CUSHMAN & DEADERICK, 1944, Jour. Paleontology, vol. 18, p. 336, pl. 52, fig. 17.—— CUSHMAN, 1946, U. S. Geol. Survey Prof. Paper 206, p. 97, pl. 40, figs. 18, 19.

Pyrulina cylindroides differs from *P. shoalcreekensis*, n. sp., in being more elongate and slender with the chambers less inflated and less embracing. It is widely recorded from Cretaceous strata and is common in the Del Rio.

Types.—Hypotypes, U.T. 1085.

PYRULINA LONGA Tappan
Plate 46, figures 7, 8

Pyrulina longa TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 114, pl. 18, figs. 2a, b.

This species is distinguished by having a fistulose growth proceeding from the apertural end. It is rarer than the other members of its genus and is not found in the upper part of the Del Rio section. Numerous small specimens are found with the fistulose growth at the end of the fourth or fifth chamber.

Types.—Hypotypes, U.T. 1086.

PYRULINA SHOALCREEKENSIS
Bullard, n. sp.
Plate 46, figures 9–12

Test small to medium in size, ovate in outline, greatest breadth near middle; acuminate at both extremities; chambers tending to become biserial, each succeeding chamber farther removed from the base, considerably embracing, last chambers much inflated; sutures depressed; margins somewhat lobulate; aperture terminal, radiate, protruding. Lengths varying from .35 mm. to .5 mm., widths, from .125 mm. to .225 mm.

Types.—Syntypes from sample 17, location C; U.T. 1087.

This species differs from *P. cylindroides* in being stouter with more inflated chambers which are more embracing and in being acuminate at both extremities. *P. shoalcreekensis* is rare in the Del Rio, occurring only in the lower samples at location C.

PYRULINA BRYKERWOODENSIS Bullard, n. sp.
Plate 46, figures 13–20

Test medium to large in size, early chambers free, later attached; early pyruline portion ovate in outline, initial end acuminate, margins smooth; final chambers attached to irregular plate-like area which is bordered by a thin transparent keel; chambers relatively few, not much inflated initially, later tending to become biserial and more inflated; wall smooth; sutures depressed to indistinct; aperture single, projecting slightly from the attachment plate, with a small hyaline neck. Lengths .425 mm. to .525 mm.; widths .2 mm. to .225 mm.

Types.—Syntypes from sample 16, location C; U.T. 1088, 1089.

No attached species of *Pyrulina* has hitherto been recorded. This species is rather common in the Del Rio in the lower levels of the section at location C. Its attachment is in general the type developed by *Globulina immobilis* and not the tubular branching form of *G. cervicornis*. *P. brykerwoodensis* may be distinguished from *G. immobilis* by the chamber arrangement and by the more irregular outline of the attachment plate; its initial chambers usually extend free from the attachment plate, while those of *G. immobilis* are generally embedded in it.

Genus PSEUDOPOLYMORPHINA Cushman & Ozawa, 1928
PSEUDOPOLYMORPHINA ROANOKENSIS Tappan
Plate 46, figures 21, 22

Pseudopolymorphina roanokensis TAPPAN, 1940, Jour. Paleontology, vol. 14, p. 113, pl. 17, figs. 22a–23, 25;—— 1943, idem, vol. 17, p. 506, pl. 81, figs. 4, 5.

This is a fistulose species of *Pseudopolymorphina* which ranges throughout the Washita and occurs with varying degrees of abundance in the Del Rio section at location C.

Types.—Hypotypes, U.T. 1091.

Subfamily RAMULININAE
Genus RAMULINA Rupert Jones, 1875
RAMULINA ABSCISSA Loeblich & Tappan

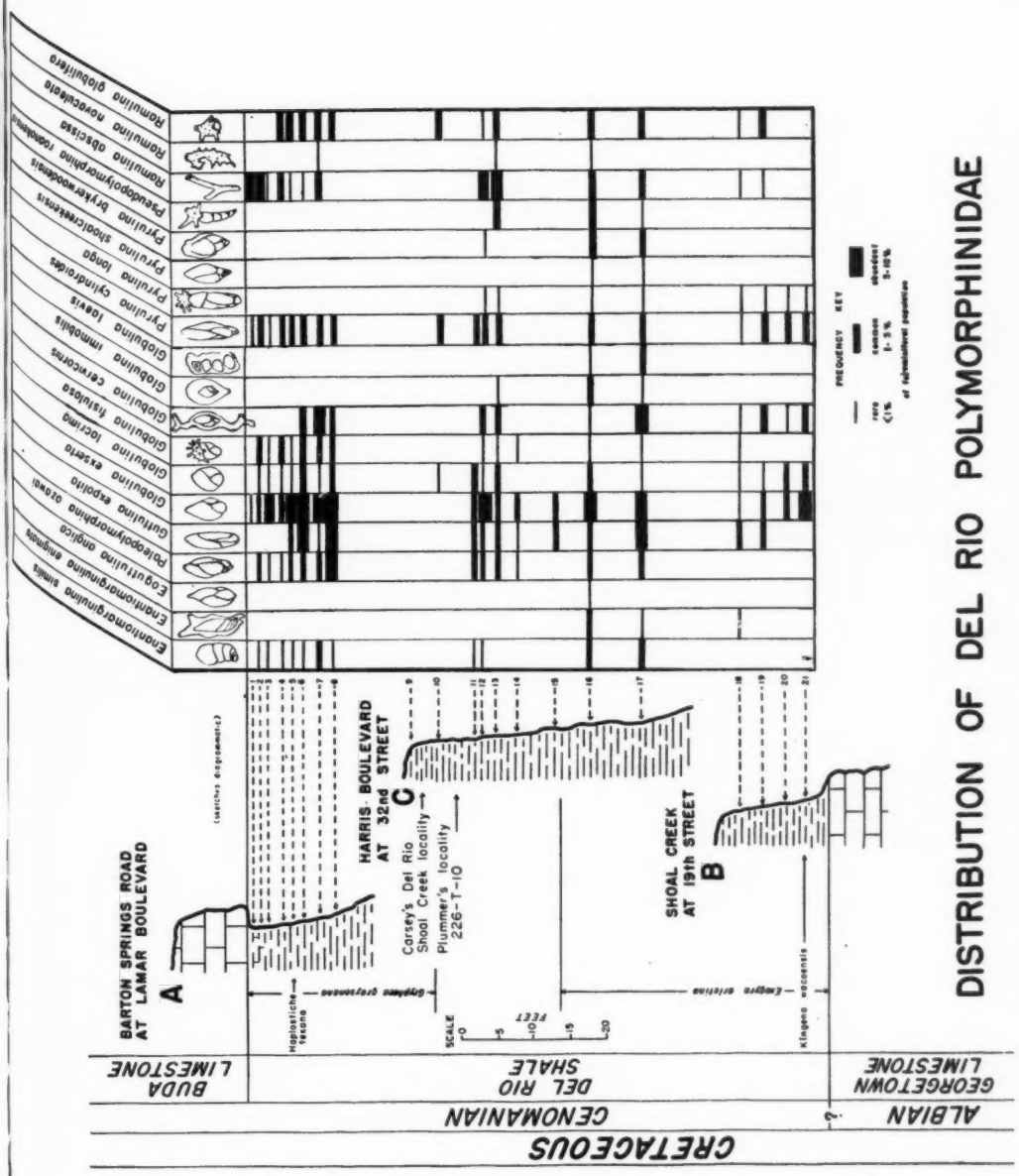
DISTRIBUTION OF DEL RIO POLYMORPHINIDAE
FREQUENCY KEY
Romulina globulifera
Romulina novocubana
Romulina obsoleta
Pseudopolymorphina texana
Pyrulina brykerwoodensis
Pyrulina shoalcreekensis
Pyrulina longa
Pyrulina cylindroides
Globulina laevis
Globulina immobilis
Globulina cervicornis
Globulina fistulosa
Globulina lacrima
Globulina exserta
Guttulina expolita
Polymorphina texana
Eoguttulina anglica
Fanniomorguluina simplex
Fanniomorguluina sinuosa
BARTON SPRINGS ROAD AT LAMAR BOULEVARD
A
HARRIS BOULEVARD AT 32nd STREET
C
Carsey's Del Rio Shoal Creek locality
Plummer's locality 226-T-10
SHOAL CREEK AT 19th STREET
B
SCALE
FEET
BUDA LIMESTONE
DEL RIO SHALE
GEORGETOWN LIMESTONE
CENOMANIAN
ALBIAN
CRETACEOUS

FIG. 1

Plate 46, figure 23

Ramulina abscissa LOEBLICH & TAPPAN, 1946, Jour. Paleontology, vol. 20, p. 254, pl. 37, figs. 7, 8.

Ramulina abscissa differs from *R. globulifera* and *R. novaculeata* in consisting of an elongate dichotomously branching tube of nearly equal diameter throughout. It is common in the Del Rio and occurs throughout the Washita.

Types.—Hypotypes, U.T. 1092.

RAMULINA GLOBULIFERA Brady
Plate 46, figures 24, 25

Ramulina globulifera BRADY, 1884, Rept. Voyage *Challenger*, Zoology, vol. 9, p. 587, pl. 76, figs. 22–28.——CHAPMAN, 1896, Roy. Micr. Soc. Jour., p. 582, pl. 12, figs. 5, 6.——TAPPAN, 1943, Jour. Paleontology, vol. 17, p. 506, pl. 81, figs. 8, 9.

Ramulina cf. *globulifera* TAPPAN, 1940, idem, vol. 14, p. 114, pl. 18, fig. 3.

R. globulifera differs from *R. novaculeata* in being finely hispid and possessing stout tubular projections, but not inflated saclike chambers. It is common at most levels in the Del Rio.

Types.—Hypotypes, U.T. 1094.

RAMULINA NOVACULEATA, Bullard, n. name
Plate 46, figure 26

Ramulina aculeata WRIGHT (not *Dentalina aculeata* D'Orbigny, 1840), 1886, Belfast Nat. Field Club Report, Proc., p. 331, pl. 27, fig. 11.—— BURROWS, SHERBORN, & BAILEY, 1890, Roy. Micr. Soc. Jour., p. 561, pl. 11, fig. 16.—— CHAPMAN, 1896 (part), idem, p. 583, pl. 12, fig. 7 (not figs. 8, 9).——EICHENBERG, 1933 (part), Niedersächs geol. Vereins zu Hannover, Jahresb. 25, Teil 1, Folge, 1, p. 18, pl. 6, fig. 6a (not fig. 6b);—— 1935, Roemer-Mus. Mitteil, no. 37, Teil 1, Folge 4, p. 29, pl. 6, fig. 1. —— TAPPAN, 1943 (part), Jour. Paleontology, vol. 17, p. 506, pl. 81, fig. 6 (not fig. 7).

Test free, small to medium in size, consisting of irregular globular to cylindrical branches extending from the inflated proloculum; wall covered with thick spines and spicules; sutures constricting; apertures rounded, at the ends of the branching chambers or at the terminal end of the proloculum. Dimensions of figured specimen: length .55 mm., width. 38 mm.

MANUSCRIPT RECEIVED JULY 7, 1952

Type.—Hypotype, U.T. 1093.

Loeblich and Tappan (1949, pp. 261–262) have pointed out that the original nomenclature of this species is in error because D'Orbigny's *Dentalina aculeata* is in fact a *Dentalina*, and, therefore, Wright's *Ramulina aculeata*, which he referred to it, has an invalid name. Hence, a new name is in order, and "*R. novaculeata*" is proposed for the species. *R. novaculeata* differs from *R. globulifera* in having large thick spines and inflated tubular chambers; it differs from *R. abscissa* in being irregularly branching, with sac-like chambers connected by narrow tubes. It is rare in the Del Rio.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 347–352, PL. 47, 1 TEXT FIG., MAY 1953

TYPE SPECIES OF *SCUTELLA**

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ABSTRACT—*Scutella subrotunda* (Leske), the type species of the genus *Scutella* Lamarck is described and figured. It is concluded that most species commonly referred to *Scutella* are not congeneric with the type. The new genera *Parascutella*, with *Scutella leognanensis* Lambert as type, and *Abertella*, with *Scutella aberti* Conrad as type, are proposed, and the genus *Parmulechinus* Lambert is revived, for species usually referred to *Scutella*.

IN 1841 Agassiz (1841, p. 5) designated *Scutella subrotunda* Lamarck as the type of the genus *Scutella* Lamarck (1816). At the same time (1841, pp. 76–78, pl. 17, figs. 1–11) he figured and described in detail certain specimens from the "Tertiary" of Bordeaux which had been identified by Lamarck as *Scutella subrotunda*. Because of the excellent character of Agassiz's figures and the authority of his work, and because of the extremely poor quality of previous figures and descriptions (Leske, 1778, pp. 206–207, pl. 47, fig. 7), Agassiz's interpretation of the species has been widely accepted and publicized (e.g., Desor, 1858, pl. 28; Nicholson, 1898, fig. 238; Zittel, 1913, fig. 405) and has influenced many systematists to assign other echinoids to this genus. From Lamarck's text (1816, p. 11) it is obvious that he considered his *Scutella subrotunda* to be the same as *Echinodiscus subrotundus* Leske, for he cites Leske's description and figures in his synonyomy. However, in 1912, Lambert called attention to the fact that the *Scutella subrotunda* illustrated by Agassiz (1841) and other authors who had followed Agassiz, was not the true *S. subrotunda* although the specimens figured (Agassiz, 1841, p. 76, pl. 17) had been identified by Lamarck as that species. At the same time Lambert reviewed at length the confusion surrounding *Scutella subrotunda*, proposed the name *Scutella leognanensis* for the species figured by Agassiz and presented a poor figure (Lambert, 1912, fig. 1) of the oral surface of a topotype of Leske's species from the Island of Malta. Lambert and Thiéry (1914, p. 317) similarly commented on the discrepancies surrounding the usage of the name *Scutella subrotunda* and applied it only to the species from Malta. Mortensen (1948, pp. 361–362) discussed the situation in a manner similar to that of Lambert, but without figuring the true *Scutella subrotunda* (Leske).

Through the good offices of Richard V. Melville of the Geological Survey and Museum (Great Britain), and the courtesy of the British Museum (Natural History), photographs and a sketch of the topotype of *Scutella subrotunda* (Leske) which Lambert (1912, fig. 1) inadequately figured, have been made available for publication while another topotype from Malta was sent to the author for examination and study. Because of the historical significance and the taxonomic importance of this species it is here described in detail.

SCUTELLA SUBROTUNDA (Leske)

Plate 47, figures 1–3; text figures 1B, 1D

Echinodiscus subrotundus LESKE, 1778, Add. ad Klein, pp., 206–207, pl. 47, fig. 7.

Scutella subrotunda LAMARCK, 1816, Hist. nat. des. anim. s. vert., vol. 3, p. 7; AGASSIZ, 1841, Mon. d'Echin., 2nd Mon., des Scutelles, pp. 76–78 (pro parte, non pl. 17, figs. 1–11); LAMBERT, 1912, Mem. Soc. Paleont. Suisse, vol. 38, fig. 1; MORTENSEN, 1948, Mon Echin., vol. 4, pt. 2, pp. 361–362.

Non *Scutella subrotunda* AGASSIZ, 1841, Mon. d'Echin., 2nd. Mon. des Scutelles, pl. 17, figs. 1–11; DESOR, 1858, Syn. des Echin. foss., pl. 28; NICHOLSON, 1898, Ancient Life-Hist. Earth., fig. 238; ZITTEL, 1913, Textb. Paleo., 2nd ed., vol. 1, fig. 405.

Test large, thin, flattened; margin moderately sharp; upper surface gently sloping from ambitus to summit, summit slightly anterior to apical system; oral surface flat;

* A Contribution from the Museum of Paleontology of the University of California, Berkeley 4, California.

ambitus angularly indented in middle of ambulacral areas, most prominently in ambulacra I and V; ambitus slightly indented at all other radial sutures, most prominently in interambulacrum 5; petals of moderate size, closed, length about half the corresponding radius; pore pairs conjugate, outer pore greatly elongated and secondarily subdivided into smaller pores (only apparent at depth); madreporite pentagonal, with four genital pores situated at apices of pentagon, two posterior genital pores farther apart than two anterior pores; periproct on oral surface, small, about midway between peristome and ambitus, situated approximately at junction between first and second pairs of post-basicoronal interambulacral plates; ambulacral food grooves with two primary branches, branching at outer end of basicoronal plates, with one or more secondary lateral branches about midway to the ambitus; peristome small, central; surface ornamented by numerous small tubercles, with a density of about 30 per linear 10 mm.; eight or nine tubercles in a single row between pore pairs in petal II; post-basicoronal plates of oral surface just in contact with basicoronal plates in all interambulacral areas; four to five post-basicoronal plates in each interambulacral column on oral surface; six to seven post-basicoronal plates in each ambulacral area on oral surface; ambulacral and interambulacral areas of approximately same width at ambitus; basicoronal plates moderately large and of approximately same size.

Dimensions of British Museum (Natural History) topotype no. E 2328: length 102.9 mm., width 105.9 mm., height 9.1 mm.

Types.—Leske's figured specimen is apparently lost; neotype, (here designated) British Museum (Natural History) no. E 16593 (specimen from which Lambert's 1912 figure was made, and here figured in Plate 47, figures 1–3); topotype, British Museum (Natural History) no. E 2328 (specimen on which above description is based).

Occurrence.—The type locality is in the Lower Coralline limestone of Malta. Information received from Dr. Richard V. Melville (personal communication, April 30, 1952) indicates that the age of these beds is still uncertain, with opinions varying from upper Oligocene to lower Miocene, but that they are probably equivalent to some of the so-called "passage beds" between the Oligocene and Miocene described by F. R. S. Henson from Palestine. Pending completion of studies now in progress, Dr. Melville advises that it is probably best to call these beds "?Oligo-Miocene."

Remarks.—This species may be readily separated from the specimens (*Scutella leognanensis* Lambert, 1912) figured by Agassiz (1841, pl. 17, figs. 1–11) and others as *S. subrotunda* by the periproct midway between the margin and the peristome, and by the shorter and more completely closed petals. In *S. subrotunda* the anterior petal is slightly longer than the two posterior petals, whereas in *S. leognanensis* the posterior petals are slightly longer than the anterior petal. From the photographs of the neotype of *S. subrotunda* it appears that the petals are somewhat more inflated than in the topotype on which the description is based, but this difference is probably without significance for much variation of this character may be found within single colonies of *Dendraster excentricus* or *Echinarachnius parma.*

Numerous studies made in the course of preparation of the section on clypeastroid echinoids for the proposed new "Treatise on Invertebrate Paleontology" have indicated that the arrangement of the plates of the oral surface of the test is of considerable taxonomic significance. Based on these studies and the examination of the topotype of *Scutella subrotunda*, the diagnosis of the genus has been revised as follows:

Genus SCUTELLA Lamarck

Scutella LAMARCK, 1816, Hist. nat. des anim. s. vert., vol. 3, p. 7; AGASSIZ, 1841, Mon. D'Echin., 2nd. Mon., des Scutelles, pp. 75–76; LAMBERT, 1912, Mem. Soc. Paleont. Suisse, vol. 38, pp. 57–61; LAMBERT & THIÉRY, 1914, Ess. Nomencl. Rais., pp. 317–319; MORTENSEN, 1948, Mon. Echin., vol. 4, pt. 2, pp. 360–362.

Type species: *Scutella subrotunda* La-

marck (subs. desig. Agassiz, 1841, p. 5) = *Echinodiscus subrotundus* Leske = *Scutella subrotunda* Agassiz (1841) pro parte (non pl. 17, figs. 1–11 = *S. leognanensis* Lambert, 1903).

Large, thin, flattened "scutellid" echinoids; petals closed, length about half the radius of test; four genital pores; peristome small, central; periproct about midway between margin and peristome; margin of test with broad indentations corresponding to sutures between all columns, most prominent posteriorly; ambulacral food grooves (Text fig. 1D) bifurcating just outside basicoronal plates, a major secondary branch about midway on primary branches; basicoronal plates moderately large, ambulacrals and interambulacrals about evenly developed; interambulacral columns all in contact with basicoronal plates, but narrower than adjacent ambulacral plates at this point; ambulacral and interambulacral columns about equal at margin; post-basicoronal plates six or seven to a column. very low near margin; periproct between first pair of post-basicoronal plates; pore pairs conjugate, the outer elongate.

As here diagnosed, few if any of the species, other than the type, which have in the past been referred to *Scutella* can be included within the genus. The position of the periproct is extremely advanced evolutionarily even though the post-basicoronal interambulacral plates are not separated from the basicoronal row. Many of the European upper Eocene and Oligocene species may be referred to the genus *Parmulechinus* Lambert (*Stenaster* Lambert, 1905, non *Stenaster* Billings, 1858) which was founded upon a young individual (*Stenaster labriei* Lambert) of *Scutella agassizi* Oppenheim (Lambert, 1915, p. 19–29), a new name for *S. striatula* Agassiz, (1841) non *S. striatula* de Serres (1829). Some of the species which appear to be referable to the genus *Parmulechinus* are *Scutella subtetragona* Grateloup, *S. lamberti* Airaghi, *S. paronai* Airaghi, *S. isseli* Airaghi, *S. melitensis* Airaghi and *S. michaleti* Lambert. This group apparently began in the lower Oligocene and became extinct in the Burdigalian.

Many of the European Miocene species which have been referred to *Scutella* appear to be congeneric with *S. leognanensis* Lambert. For these species the new genus *Parascutella* is here proposed:

Genus PARASCUTELLA Durham, n. gen.

Scutella auctores, non Lamarck, 1816.

Type species: *Scutella leognanensis* Lambert (1903), (Text fig. 1A) = *S. subrotunda* Agassiz (partim) (1841, pl. 17, figs. 1–11), non *Echinodiscus subrotundus* Leske.

Large, thin, "scutellid" echinoids; petals moderately closed, length about two-thirds radius of test; a tendency for anterior petal to be shorter than posterior petals; pore pairs conjugate; four genital pores; peristome moderately small, central; periproct submarginal, often with a groove to anal notch in margin of test; margin of test with broad indentations corresponding to all sutures, most prominent posteriorly; ambulacral food grooves of scutellid type, bifurcating just outside basicoronal plates; basicoronal plates moderately large, ambulacrals and interambulacrals about equally developed; interambulacral columns all just barely in contact with basicoronal interambulacral plates; four to five post-basicoronal plates in each interambulacral column on oral surface, about half as high as wide near ambitus; periproct situated along suture between third pair of post-basicoronal plates; ambulacral and interambulacral areas of about equal width at margin.

The type species is from the Burdigalian of southern France. *Scutella neuvillei* Lambert is an Aquitanian species that is probably referable to this genus. *S. almerai* Lambert and *S. gibbercula* de Serres, from the Tortonian appear to be the youngest species belonging in the genus. It is somewhat uncertain whether forms like *Scutella truncata* Valenciennes of Agassiz (1841, pl. 16, figs. 1–10), *S. faujasii* de France (Agassiz, 1841, pl. 15, figs. 4–6) and *S. propinqua* Agassiz (ibid, pl. 16, figs. 11–16) should be considered in this genus or be assigned to a new genus. They are similar to *Parascutella* except that the periproct is farther from the margin and situated along the

suture between the second and third post-basicoronal plates.

Insofar as now known the three preceding genera are restricted to European areas, although additional information may show that they were also found in more eastern parts of the Tethyan seaway.

Along the east coast of the United States and in the Caribbean area another group of species that have been referred to *Scutella* occur. They are all closely related to *S. aberti* Conrad. For these the new genus *Abertella* is proposed.

Genus ABERTELLA Durham, n. gen.

Type species: *Scutella aberti* Conrad (Text fig. 1C).

Large, thin, scutellid echinoids, rounded anteriorly, but with a moderately large posterior anal notch and broad marginal indentations in ambulacra I and V, shallower indentations corresponding to remaining ambulacra; petals elongate, moderately closed, length about two-thirds radius of test; pore pairs conjugate, poriferous zones as wide or wider than interporiferous zones; four genital pores; peristome of moderate

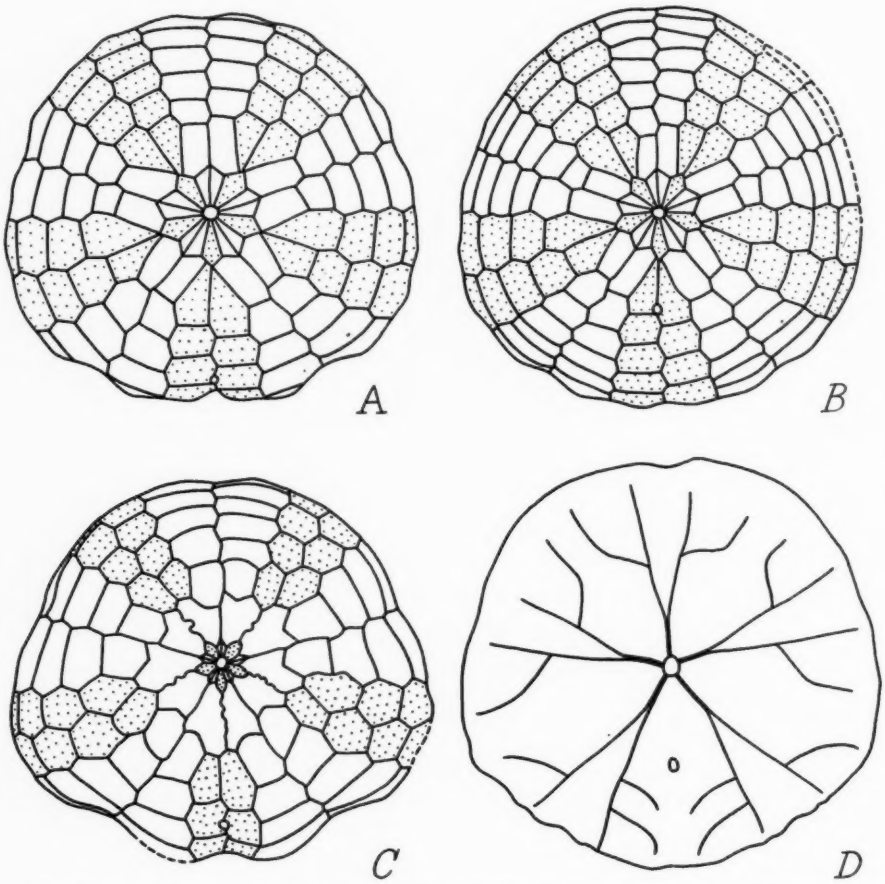

FIG. 1—*A. Parascutella leognanensis* (Lambert), ×0.56. Oral surface (after *Scutella subrotunda* Agassiz, 1841, pl. 17, fig. 2); *B. Scutella subrotunda* (Leske), ×0.54. Oral surface. Topotype, British Museum (Natural History) no. E 2328; *C. Abertella aberti* (Conrad), ×0.42. Oral surface. Hypotype, Johns Hopkins University, Department of Geology; *D. Scutella subrotunda* (Leske), ×0.57. Food grooves on oral surface. Neotype, British Museum (Natural History) no. E 16593.

size, central; periproct submarginal, sometimes as much as one-eighth distance from margin (apparently dependent on depth of anal notch), situated along suture between second pair of post-basicoronal interambulacral plates; ambulacral food grooves of scutellid type but bifurcating closer to peristome than in *Parascutella;* basicoronal plates moderately small, ambulacral plates considerably larger and rounder than interambulacral plates; interambulacral columns widely separated from basicoronal interambulacral plates by first post-basicoronal ambulacral plates; on oral surface three to four post-basicoronal plates in each interambulacral column, five to seven post-basicoronal plates in each ambulacral column; interambulacral areas only about one-half as wide as ambulacral areas at ambitus.

Scutella floridana Cooke, *S. cazonesensis* Kew, and *S. habanensis* Sanchez Roig are other species to be referred to this genus. Kew was uncertain as to the exact age of his species, but in view of its similarity to *S. floridana,* it would appear that it is probably of Helvetian age also. *S. habanensis* Sanchez Roig was referred to the "Oligo-Miocene" at the time of description, and in keeping with its older age appears to be somewhat more primitive than the other species referred to the genus for the posterior indentations of the test are less accentuated. In view of the fact that the other three species are apparently of Helvetian age, it is probable that *S. habanensis* is also from beds of Miocene age, rather than "Oligo-Miocene" age.

Abertella is easily separable from the European *Scutella* and *Parascutella* by its widely interrupted interambulacral areas on the oral surface. None of the Pacific Coast species referred to *Scutella* by Kew and others are at all closely related.

The relationship of *Echinarachnius sebastiana* Jackson (1922, pp. 48–50, pl. 7, figs. 5, 6, text fig. 4), from the Oligocene of Porto Rico, to *Abertella* needs to be investigated, but no specimens were available for the present study.

Scaphechinus mirabilis Agassiz, living in Japanese waters, has at various times been referred to *Scutella* but it is readily separable by the post-basicoronal interambulacral plates being widely separated from the basicoronal row.

The four genera discussed here may be separated by the following characters:

Scutella: periproct midway on oral surface, between first pair of post-basicoronal interambulacral plates; petals closed, about one-half length of corresponding radius, anterior petal longest; on oral surface interambulacral areas narrowing towards basicoronal row and in contact with it; margin of test only moderately indented.

Parascutella: periproct submarginal, along suture between third pair of post-basicoronal interambulacral plates; petals nearly closed, about two-thirds as long as corresponding radius, anterior petal shortest; on oral surface interambulacral areas narrowing towards basicoronal row and in contact with it; margin of test only moderately indented.

Abertella: periproct immediately submarginal, between second pair of post-basicoronal plates; petals moderately closed, about three-fourths length of corresponding radius, anterior petal shortest; on oral surface interambulacral areas narrowing towards basicoronal row and widely separated from basicoronal row; in basicoronal row ambulacral plates larger than interambulacral plates; posterior margin of test with a well-developed anal notch.

Parmulechinus: periproct submarginal, about seven or eight pairs of interambulacral plates between it and basicoronal row; petals nearly closed, one-half to five-eighths length of corresponding radius, all petals subequal; on oral surface interambulacral areas tend to maintain their width as they approach the basicoronal row while ambulacral areas narrow sharply (the reverse of the condition found in other scutellids) towards basicoronal row. Margin of test with broad, moderately deep (except anteriorly) indentations in ambulacral areas.

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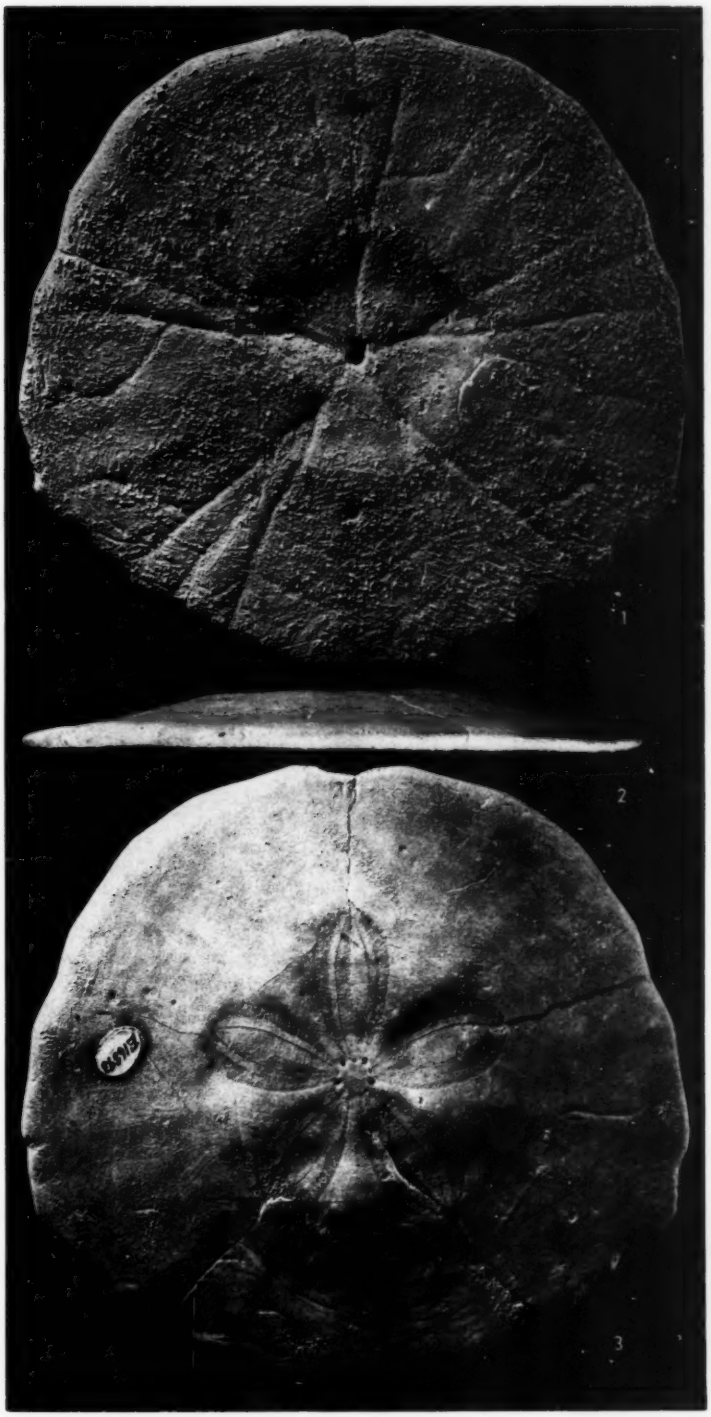
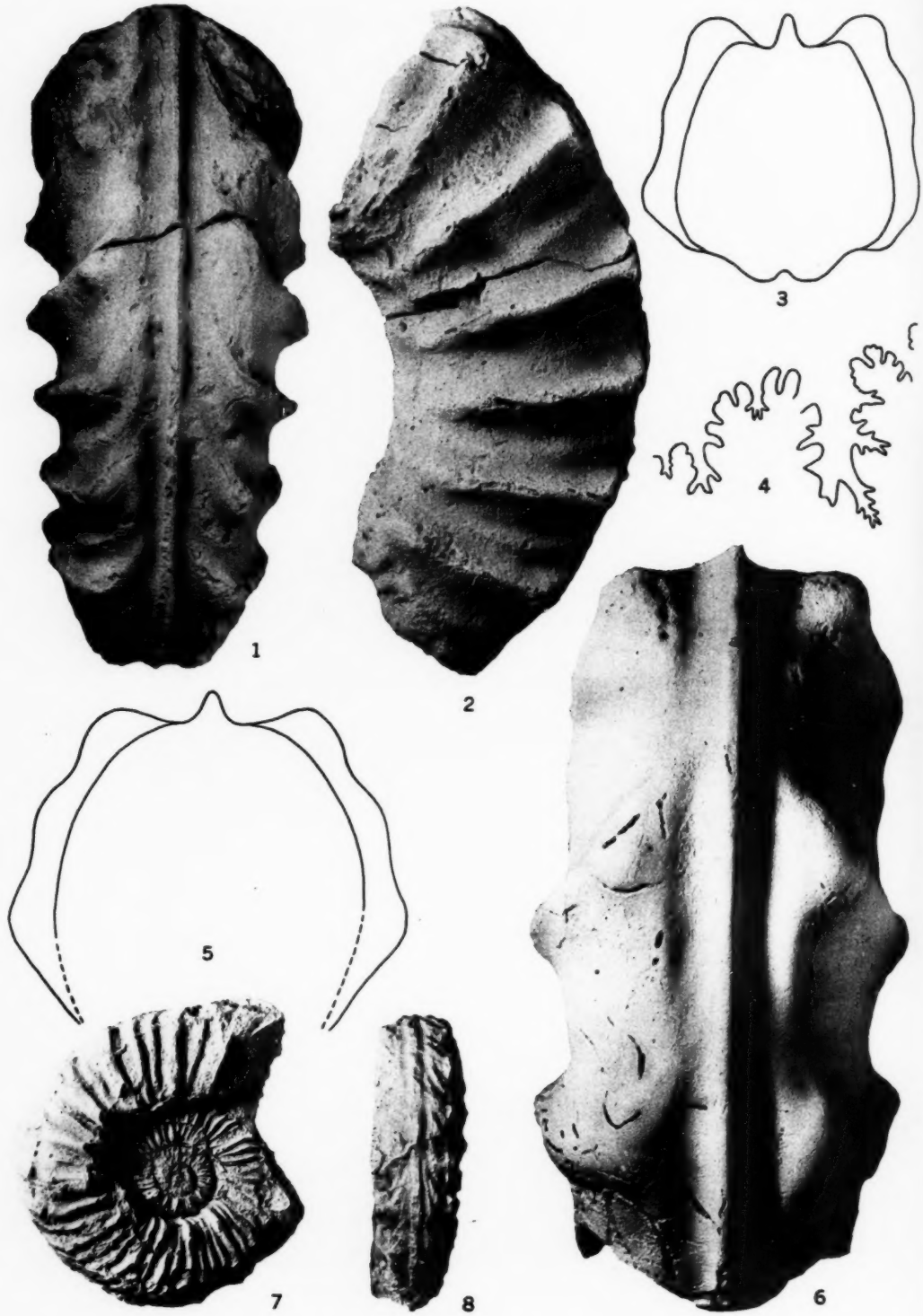
MANUSCRIPT RECEIVED JULY 1, 1952

EXPLANATION OF PLATE 47

FIGS. 1–3—*Scutella subrotunda* (Leske), ×0.85. Neotype, British Museum (Natural History) no. E 16593, from "?Oligo-Miocene," Island of Malta. *1*, oral view, *2*, lateral profile from right side, *3*, apical view. Photograph courtesy British Museum (Natural History).



Durham, type species of *Scutella*



Cobban, Upper Cretaceous *Prionocyclus*

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 353–355, PL. 48, MAY 1953

A NEW SPECIES OF *PRIONOCYCLUS* FROM UPPER CRETACEOUS CARLILE SHALE[1]

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ABSTRACT—*Prionocyclus quadratus*, n. sp., is the youngest known species of the ammonite genus *Prionocyclus* in the western interior of the United States. It is probably latest Turonian. The species occurs in the Sage Breaks member and uppermost part of the Turner sandy member of the Carlile shale of the Black Hills region and in the equivalent rocks along the western margin of the Powder River basin, Wyoming. *Prionocyclus quadratus* is closely related to its immediate ancestor *P. reesidei* Sidwell.

INTRODUCTION

COLLECTIONS of ammonites from the upper Turonian Sage Breaks member of the Carlile shale of the north and east flanks of the Black Hills reveal the presence of a robust new species of *Prionocyclus*. Fossils, which are scarce in the Sage Breaks member, occur in highly septarian calcareous concretions. The fossils are commonly crushed and nearly always fragmented by the calcite veins that extend throughout the concretions. Enough undeformed fragments of the new prionocyclid are now at hand to warrant its description and recognition as a guide fossil. This species, *P. quadratus*, appears to range throughout the the Sage Breaks member and down into the uppermost part of the Turner sandy member of the Carlile shale. Fragments of 25 individuals from the Sage Breaks member and 15 from the Turner sandy member were available for study. The specimens from the Turner member, although more complete than those from the Sage Breaks member, are considerably distorted by thick septarian veins of calcite. In addition to these Black Hills specimens, fragments representing about 15 individuals from the west flank of the Powder River basin are at hand.

The types are at the United States National Museum in Washington. The photographs were made by Nelson A. Shupe, United States Geological Survey.

PRIONOCYCLID ZONES OF THE CARLILE SHALE

The Carlile shale attains its maximum known thickness and its most completely fossiliferous development on the north flank of the Black Hills in southeastern Montana and western South Dakota (Cobban, 1951, pp. 2187–2190). There the Turner sandy member contains *Prionocyclus macombi* Meek in the lowest part, *P. wyomingensis* Meek and its varieties in the middle part, and *P. quadratus*, n. sp., in the uppermost part. These mark clearly separate

[1] Publication authorized by the Director, United States Geological Survey.

EXPLANATION OF PLATE 48

All figures natural size.

FIGS. *1–8*—*Prionocyclus quadratus* Cobban, n. sp. *1–3*, ventral and side views and cross section of holotype USNM 108332 from Sage Breaks member of Carlile shale, Carter County, Montana. *4*, first and second lateral lobes of the suture at diameter of 130 mm. of paratype USNM 108335 from a bed near top of Turner sandy member of Carlile shale 6.5 miles north of Belle Fourche, South Dakota. *5*, *6*, cross section and ventral view of paratype USNM 108333a from same locality as holotype. *7*, *8*, side and ventral view of paratype USNM 108334, an immature specimen from the Sage Breaks member 9 miles southeast of Rapid City, South Dakota.

faunal zones each having distinctive species of *Scaphites* and *Inoceramus*. Between the beds containing *P. wyomingensis* and *P. quadratus* are rocks carrying *Scaphites nigricollensis* Cobban, a species intermediate between *S. whitfieldi* Cobban, which occurs with *P. wyomingensis*, and *S. corvensis* Cobban, which occurs with *P. quadratus*. A diagnostic prionocyclid fauna has not been found in this *S. nigricollensis* zone. In the Frontier formation in south-central Wyoming, however, *P. reesidei* Sidwell, a form intermediate in character between *P. wyomingensis* and *P. quadratus*, occurs above rocks containing *P. wyomingensis* (Cobban and Reeside, 1951, text fig. 2). Along the west flank of the Powder River basin *P. quadratus* has been found in septarian concretions in the noncalcareous shale immediately above the Wall Creek ("First") sandstone member of the Frontier formation. The shale immediately below the Wall Creek sandstone member contains *P. wyomingensis*. *Prionocyclus* has been found in the Wall Creek member at only two localities. Near Kaycee a fragment referable to *P. quadratus* was found as float from the sandstone, and about 65 miles farther south several specimens of *P. reesidei* were collected from a bed near the base of the Wall Creek sandstone member. Considering these occurrences, it is clear that *P. quadratus* and *P. reesidei* occur above *P. wyomingensis* and that *P. reesidei* is probably an older species than *P. quadratus*. It seems probable that further collecting will reveal *P. reesidei* in the *Scaphites nigricollensis* zone of the Black Hills.

SYSTEMATIC DESCRIPTION

PRIONOCYCLUS QUADRATUS Cobban, n. sp.

Plate 48, figures 1–8

Whorl section quadrate to subquadrate at all growth stages; umbilical wall steep in early stages, but more gently inclined in late stages. Early whorls densely ribbed, with primaries and secondaries of near equal strength; later whorls more sparsely ribbed, with secondaries inconspicuous or absent. Primary ribs gradually increase in strength as growth continues; bear radially elongate umbilical nodes and subconical ventrolateral nodes, and, on adult whorls, low incipient mid-flank nodes. Suture moderately incised.

At the smallest diameter observed, 5 mm. (pl. 48, fig. 7), the conch is distinctly ribbed. The ribs are nearly equal in strength, inclined forward slightly, and number about 30 per whorl. Between diameters of 5 and 30 mm. the rib density increases to more than 40 per whorl, and every third or fourth rib (primary) bears radially elongate umbilical nodes and subconical ventrolateral nodes. The ribs become somewhat flexuous. Each rib is inclined backward on crossing the umbilical wall, bends sharply at the umbilical shoulder, crosses the flank in a slightly sinuous manner and in a prorsiradiate direction, and bends again sharply forward at the ventrolateral shoulder. Up to a diameter of 30 mm. the ribs are of nearly equal strength, but at greater diameters the primaries become stronger, whereas the secondaries become weaker and fewer. By a diameter of 120 mm. the umbilical wall has become less steep, the ribs have become straighter although still forwardly inclined, and the secondaries are reduced to one or two scarcely discernible intercalated ribs between the primaries. At diameters greater than 120 mm. the secondary ribs disappear and the number of ribs (primary) per whorl declines to about 25 for a conch 200 mm. in diameter. In this late stage each primary rib crosses the umbilical wall as an inconspicuous low ridge that trends in a slightly rursiradiate direction. At the umbilical shoulder the rib curves forward and rises into a prominent radially elongate node that marks the greatest width of the whorl (pl. 48, fig. 5). From this node the rib continues across the flank fairly straight although forwardly inclined. At the middle of the flank it is elevated into an obscure incipient radially elongate node. At the ventrolateral shoulder the rib terminates in a large blunt node. In the young stages, the keel is densely serrate, but in the older stages the serrations become shallower and farther apart, or the keel may be smooth.

None of the specimens in the type lots or in the other collections from the Black Hills indicate a very large species. The largest fragments, all nonseptate, came from individuals less than 250 mm. in diameter.

On the other hand, specimens from the west flank of the Powder River basin that seem referable to this species are much larger, with some being entirely septate at diameters of 250 mm.

Remarks.—This species is easily distinguished by the adult whorls with quadrate section, incipient mid-flank nodes, and large blunt ventrolateral nodes. It appears to be derived from and most closely related to *Prionocyclus reesidei* Sidwell (1932, p. 318, pl. 49. figs. 10–12). The adult of that species differs chiefly by its whorls with quadrangular cross section. The inner whorls (holotype) of *P. reesidei* figured by Sidwell are much more coarsely ribbed than comparable stages of *P. quadratus*, and the proportion of primary to secondary ribs is entirely different. The writer has at hand 25 specimens of *P. reesidei* from the type locality. The adult shells are all more compressed laterally, and, in general, more densely ribbed than the adult shells of *P. quadratus*. An older form, *P. wyomingensis* Meek var. *robusta* Haas (1946, pp. 201–216, text figs. 92, 105–107, pl. 20, figs. 3, 6, 7; pl. 21, figs. 4, 6; pl. 22, figs. 3–5; pl. 23, fig. 2), resembles *P. quadratus* by its quadrate whorl section, but this variety differs by its different-shaped cross section, denser costation, double ventrolateral nodes, and lack of an incipient mid-flank node. The fragment of a large prionocyclid from New Mexico, first figured by Haas (1943) as *Pervinquieria* cf. *romeri* Haas, but later referred by him to *Prionocyclus* (1944), and then to *Prionocyclus* cf. *wyomingensis* (1946, pp. 200, 215, 219, pl. 23, figs. 1, 3), may possibly be *P. quadratus*. *Prionocyclus guayabanus* (Steinmann) Gerhardt (1897, p. 197, text fig. 19, pl. 5, figs. 22a–c) from the Cretaceous of Colombia has as stout a whorl section as *P. quadratus*, but lacks incipient mid-flank nodes and the ribbing is much less pronounced. Other species of *Prionocyclus* may be readily distinguished from *P. quadratus* by their laterally compressed whorls, denser ribbing, or double ventrolateral nodes.

Occurrence.—The types are from the Sage Breaks and Turner members of the Carlile shale of the north and east flanks of the Black Hills. The species occurs all through the Sage Breaks member and through at least the upper 20 feet of the underlying Turner sandy member. Other specimens have been collected from calcareous septarian concretions 30 to 40 feet above the Wall Creek sandstone member of the Frontier formation at localities 4 miles northwest, 1.5 miles southwest, and 7.5 miles southeast of Kaycee, Wyoming, and from similar concretions 12 miles south-southwest of Buffalo, Wyoming.

Types.—Holotype USNM 108332, figured paratype USNM 108333a, and two unfigured paratypes USNM 108333b–c, are from the Sage Breaks member in sec. 33, T. 9 S., R. 61 E., Carter County, Montana. Their position within the member is not known. Figured paratype USNM 108334 is from a septarian concretion bed 42 feet above the base of the Sage Breaks member 9 miles south-southeast of Rapid City, in NE¼ sec. 22, T. 1 S., R. 8 W., Pennington County, South Dakota. Figured (suture only) paratype USNM 108335 is from a septarian concretion bed 17 feet below the top of the Turner sandy member 6.5 miles north of Belle Fourche, in E½ sec. 2, T. 9 N., R. 2 E., Butte County, South Dakota.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 356–444, PL. 49, 6 TEXT FIGS., MAY 1953

CAUSES AND PALEOECOLOGICAL SIGNIFICANCE OF DWARFED FOSSIL MARINE INVERTEBRATES

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ABSTRACT—A "typical" dwarfed assemblage, the limonitic Pennsylvanian "Dry shale fauna" is studied. Approximately 4,000 specimens were collected in Lyon, Greenwood, and Elk Counties, Kansas. Five new genera are established. The fauna consists of 21 species, 11 of which are new. The ecology of the Dover shale and Dry shale seas is reconstructed, based on lithologic and faunal data. The gray argillaceous muds deposited in such seas contain the limonitic fauna. In Elk County limonitic fossils occur above the coal. Catastrophic death and restricted environment are postulated.

Seven thousand individual measurements were made on usable fossils. These were then tallied on the Wentworth scale, permitting an effective size-grade analysis. The major grade-size was thus determined. Juveniles and adults were distinguished by morphologic criteria, graphic-analysis, and the use of the known upper size limit for any given genus or species. The evidence on dwarfism for 15 species is conclusive. For six species, due to small sample or poor preservation, it is inconclusive. Only adult imitoceratids appear to be true dwarfs. All other faunal components consist of immature forms and/or undwarfed adults.

The assemblage is termed a "pebble necrocoenosis" (8–4 mm.) indicating that sedimentary processes (sorting) and not biological processes (growth retardation) have led to the observed relative size uniformity.

Biological evidence and theories on growth in marine invertebrates are applied to the paleontological problem of dwarfism. The evidence includes: experimental growth acceleration (diatoms, algae, protozoans) by previously frozen water (trihydrol) and the independently observed latitudinal size increase in marine invertebrates; experimentally controlled size variation with changing salinity, etc.; explanation of growth-retarding effects of iron and *oligodynamik* waters; *Pufferwirkung* to explain normal-sized pyritized faunas; physiological effects of phosphates; retarding effects on cell growth of the sulfhydryl group.

Suppression of terms "dwarf," "depauperate," "diminutive" to designate small size of a fauna is proposed. Pebble-necrocoenosis (psephonecrocoenosis) is the suggested substitute.

INTRODUCTION

THE present investigation was undertaken with a view to contributing some solutions to the problem of dwarf fossil marine invertebrates. The following questions were raised:

1) How can a "dwarf" fauna be recognized as such?

2) Are the designations "dwarf," "depauperate," "diminutive" for faunas described in the literature, valid designations?

3) What light can researches of modern biology throw on (a) The factors affecting growth, particularly retardation of growth, (b) Size distributions within living marine invertebrate species?

4) Based on answers obtained for questions 1–3, what are the probable causes and paleoecologic significance of "dwarf" marine invertebrates found in the fossil record.

A critical study of the literature, which is discussed in some detail, revealed many unresolved problems pertaining to dwarf faunas. These appeared to stem from unsystematic procedures employed in their determination. It thus became apparent that before any meaningful statements could be made regarding the "dwarfed" character of a fauna, a methodology would have to be developed and tested. To further this end, the following plan was proposed:

Assuming that any fauna previously referred to in the literature as "dwarf" should be suitable as a "type fauna" for this study,

1) Collect as many representatives of this fauna from known or determinable horizons as possible.

2) Describe and figure all elements of this fauna not previously described.

3) Reconstruct the ecology of the environment in which this fauna lived or into which it migrated or was transported.

4) Obtain a documented answer to the question, "Is this fauna or are any of its elements dwarfed?"

Utilizing the answers obtained to the preceding questions as a frame of reference,

5) Reexamine the literature on dwarf faunas to determine if any such faunas have been established by critical procedures.

6) In the light of the evidence of the biological sciences, consider the causes and paleoecologic significance of dwarfed elements within any marine invertebrate fauna.

The above plan was carried out step by step. Collections of the limonitic fauna were made by the writer during July and August of 1951 from exposures of the Dover shale member and the Dry shale (formation?) in Lyon, Greenwood, and Elk Counties of Kansas. Research on the theoretical aspects of the study was started in February, 1951.

To facilitate presentation of the evidence, the present study is divided into two major parts: Part I—Fauna and Paleoecology of the Pennsylvanian Dry Shale of Kansas, Part II—Theoretical Aspects of the Problem of Dwarf Fossil Marine Invertebrates. Data accumulated for the execution of points 1–4 of the plan described above constitute the subject matter of Part I. Points 5 and 6 of the plan are treated in Part II.

Part I—Fauna and Paleoecology of the Pennsylvanian Dry Shale of Kansas

Materials and procedures.—Approximately 4,000 fossils of the "Dry shale fauna" were available for this study. A large part of these were collected by the writer. The remainder were available in the museum collections of the State University of Iowa.

The bulk of the fauna was found weathered out of shaly rock matrix but a small portion (particularly ostracods) was obtainable only after disaggregating and sieving.

Each of the 4,000 fossils was carefully examined under the binocular microscope and a rough sorting made into usable and unusable specimens. The result was 1,802 usable fossils segregated by species and locality.

Critical dimensions were obtained for each of the 1,802 fossils by use of a micrometer eyepiece (100 divisions in 10 mm.) attached to a binocular microscope. Approximately 7,000 individual measurements were recorded, with an average of four per specimen.[1]

Localities.—(Lyon County): *Dry N.*—Sec. 13, T. 16 S., R. 12 E., cut South of Price's Pond, 4 miles East of Admire Jct., Kansas. *Dry E-1.*—Sec. 10, T. 19 S., R. 11 E., cornfield opposite Thompson's ranch-type house, directly S. of W. 18th Street, Emporia, Kansas and opposite Emporia Golf Course. *Dry E-1a.*—includes the following: bank on right side of road entering park immediately south of Emporia Golf Course; ditch on golf club side of road; various exposures of Dover throughout park near entrance. *Dry E-2.*—shale bank to right of road entering Country Club Heights, Emporia, Kansas. *Dry E-3.*—starting from entrance to park on East 16th Avenue, 213 ft. ± NW along Highland Avenue, Emporia, Kansas on park side. *Dry E-4.*—South of Sardis Church (Sardis Church Road), 2 miles W. of Emporia airport, road banks. *Dry E-5.*—Sec. 5, T. 19 S., R. 11 E., ("type locality") top and ledges of knoll near Dry Creek.

(Greenwood County): *Dover P-1.*—SW cor. $SE\frac{1}{4}SW\frac{1}{4}SW\frac{1}{4}$ Sec. 5, T. 28 S., R. 10 E., cornfield right side Hwy. K-96 going W., 1½ miles NE. of Piedmont, Kansas. *Dover P-2.*—330 ft. W. of Dover P-1, left side of Hwy. *Dover P-3.*—$WL/NW\frac{1}{4}NW\frac{1}{4}NW\frac{1}{4}$ Sec. 8, T. 28, S. R. 10 E., road ditches on both sides going S. from Hwy. K-96.

(Elk County): *Dry C-1.*—c/EL $SE\frac{1}{4}SE\frac{1}{4}SE\frac{1}{4}$ Sec. 2, T. 30 S., R. 9 E. *Dry C-2.*—c/SL $SE\frac{1}{4}SE\frac{1}{4}SE\frac{1}{4}$ Sec. 9, T. 31 S., R. 9 E. *Dry C-3.*—NE cor. $NE\frac{1}{4}NW\frac{1}{4}NW\frac{1}{4}$ Sec. 29, T. 31 S., R. 9 E.

[1] Tabulation of all measurements are given in Appendix A, pages 216 to 244 of the original manuscript which is on file in the Geology Library of the State University of Iowa.

LITHOLOGY AND FAUNAL DISTRIBUTION BY LOCALITIES

Dry N.—The Dry shale is almost completely weathered away except superficially directly above the Dover limestone fusulinid (*Triticites*) bed. The single Dry shale fossil found was a badly weathered brachiopod, *Crurithyris planoconvexa*. Gray-to-black shaly soil overlying limestone contains numerous ironstone concretions and pebble size pellets; below the fusulinid phase about 12–16 inches of gray clayey shale.

Dry E-1.—Gray to dark-gray argillaceous shale occurring between and at the base of cornstalks: limonitic fossils abundant, detrital content greater than 10%, subround to subangular mostly clear, but some rose and milky detrital quartz 1-1/4 mm., smaller quantities of subangular smoothfaced tan and white detrital chert 1–½ mm. and coarser, minor quantities of: coal constituents 4–2 mm., of two types, fibrous and chunky, flat-to-chunky and subangular hematite and limonite granules, fragments of Dover limestone containing large calcareous Bryozoa, brachiopods, and crinoid stems, or these fossils weathered out. The limonitic fauna found on the surface consists of: *Imitoceras grahamense, Goniloboceras goniolobum, Crurithyris planoconvexa, Nuculana bellistriata, Anthraconeilopsis kansana, Pleurophorus? dryensis, Kansana discoidalia, Strobeus* cf. *paludinaeformis, Euphemitella emrichi, Bellerophon wabaunseensis.*

Dry E-1a.—Gray to dark-gray argillaceous to silty shale, in some places completely weathered away leaving typical limonitic fauna exposed on surface of Dover limestone in pits and pockets. Fauna included: *Imitoceras grahamense, Goniloboceras goniolobum, Crurithyris planoconvexa, Nuculana bellistriata, Anthraconeilopsis kansana, Schizodus piedmontensis, Aviculopecten* sp. undet. I, *Pleurophorus pseudoblongus, Kansana discoidalia, Euphemitella emrichi, Straparolus* (*Euomphalus*)? *gladfelteri, Bellerophon wabaunseensis.*

Dry E-2.—3. Shale bank, upper 10 inches, same lithology as lower ten inches with addition of some iron carbonate partings or crusts; contains a limonitic and calcareous or iron stained calcareous molluscan-ostracod fauna including: *Anthraconeilopsis kansana, Nuculanella piedmontia* and several unidentified ostracod fragments, Bryozoa and gastropods.

2. Shale bank, lower 10 inches, light gray, very soft, argillaceous shale, finely laminated, light limonitic stain, coal fragments; contains limonitic and iron-stained calcareous molluscan-ostracod fauna including: *Nuculanella piedmontia, Neobeyrichiopsis emporiensis, Bairdia subconvexa, Bairdia beedei, Hollinella dissimilis, Hollinella gibbosa.*

1. Channel through shale excavated 26 inches below base of shale bank to contact with Dover or Grandhaven limestone; 5 inches above contact with limestone containing the fusulinid *Triticites*, a dark, wide limonite-hematite band encountered.

Dry E-3.—Dark gray to black shaly soil along footpath contained the following fossils: *Kansana discoidalia, Schizodus piedmontensis, Pleurophorus? dryensis, Anthraconeilopsis kansana, Nuculana bellistriata, Goniloboceras goniolobum, Imitoceras grahamense.*

Dry E-4.—Dark gray to black shaly soil contained the following fossils: *Strobeus* cf. *paludinaeformis, Goniloboceras goniolobum, Imitoceras grahamense.*

Dry E-5.—Dark gray to black shaly soil contained: *Imitoceras grahamense, Goniloboceras goniolobum, Strobeus* cf. *paludinaeformis, Euphemitella emrichi, Straparolus* (*Euomphalus*)? *gladfelteri.*

Dover P-1.—Between and at base of corn stalks, limonitic fossils abundantly exposed on shaly soil surface: Dark gray argillaceous shale with about 5% limonite and hematite mostly as pellets but some as subangular chunks and flat smooth discs 1–¼ mm. to 4 mm., occasional limonitic crust to 9 mm., minor quantities of: cloudy and clear detrital quarts 1–½ mm., fragmented calcareous fossils, coal constituents, detrital red chert. The limonitic fauna included: *Imitoceras grahamense, Goniloboceras goniolobum, Crurithyris planoconvexa, Nuculana bellistriata, Anthraconeilopsis kansana, Pleurophorus? dryensis, Schizodus piedmontensis, Aviculopecten* sp. undet. II. *Nuculanella piedmontia, Pleurophorus pseudoblongus, Kansana discoidalia, Euphemitella emrichi, Straparolus* (*Euomphalus*)? *gladfelteri.*

Dover P-2.—Dover is 25 inches thick,

immediately above limestone the following Dry shale fossils were found in the soil: *Nuculanella piedmontia, Nuculana bellistriata, Imitoceras grahamense.*

Dover P-3.—Weathered out of dark gray to black shaly soil, the following fossils occurred: *Bellerophon wabaunseensis, Euphemitella emrichi, Nuculanella piedmontia, Anthraconeilopsis kansana, Nuculana bellistriata, Crurithyris planoconvexa, Goniloboceras goniolobum, Imitoceras grahamense.*

Dry C-1.—

Bed Number		Thickness (In Feet)
5	Massive, clastic limestone, characteristic tawny brown weathering of "Grandhaven formation" containing productid brachiopods and other types of brachiopods, bryozoans, crinoid stems, gastropods; about 2–3 per cent silt size detrital quartz; fossil content greater than 10 per cent of the rock	1.16
4	Gray weathering, thin-bedded, fossiliferous calcareous siltstone; hydromicas present but infrequent; upper part of lowermost third a clastic limestone containing same brachiopods, crinoid stems, etc. as Bed No. 5	1.50
3	Brown-to-gray weathering calcareous siltstone, hydromicas more frequent than in Bed No. 4, this bed is arbitrarily subdivided into three parts each 5 inches thick:	
	c) Pustulate *Myalina*-type pelecypods (Species A) poorly preserved, length $2\frac{7}{8}$ inches, width, $2\frac{1}{4}$ inches, crinoid stems.	
	b) *Myalina*-productid zone, about 2 inches above top of Bed No. 3a. Rugose type *Myalina* (Species B), length $2\frac{3}{4}$ inches, width $1\frac{7}{8}$ inches.	
	a) Calcareous and limonitic partings, some disseminated coal fragments, more argillaceous than Bed Nos. 3c or 3b, contains small calcareous brachiopods and other calcareous fossil fragments	1.25
2	Soft, poorly consolidated coal bands (0.35–0.50 mm. thick), with argillaceous-to-silty microfacies, some iron oxide stain	0.29
1	Loosely consolidated siltstone containing gastropods and ostracods, both with calcareous tests, deep iron oxide stain	0.58
	Total Thickness	4.78

Dry C-2.—Three distinct units were recognizable: the lowermost unit, Dover limestone, characterized by a small corallite, *Dibunophyllum exiguum?* (See Jeffords, 1948: 619–620), and containing crinoid stems; above that, a residual brown-black shaly soil (Dry shale) approximately one foot thick and containing a limonitic and a calcareous specimen of *Euphemitella emrichi*. The third unit above the shaly soil horizon was a massive clastic limestone containing fossils of the type found in the Grandhaven (cf. Bed No. 5, Loc. Dry C-1).

STRATIGRAPHY OF THE PENNSYLVANIAN DRY SHALE

The Dry shale [upper part of Virgilian Series (Stage? cf. Moore, 1950, p. 9, fig. 2) Wabaunsee group] as defined by Moore et al. (1934, 1951) and Moore (1935, 1949) occupies a stratigraphic interval between the Dover limestone below, and the Grandhaven limestone above. The formation was formerly an undifferentiated part of Adam's "Emporia limestone" (1903: 52) and later of the "Admire shale" of Haworth and Bennett (1908; Moore, 1935, p. 49, fig. 11).

The Dry shale may be placed in the context of the two cyclothems of which its members are a part. When this is done, the basal shale member (Index number .8–.9)[2] occurs as the last member of the Dover cyclothem, stratigraphically above the uppermost of three limestone members of the Dover limestone formation. The three Dover limestone members, molluscan, fusulinid, and locally algal, respectively, are separated by two shale members. Based on the ideal Wabaunsee cyclothem (Moore, 1935: 25), the rest of the Dry shale (Index number .0–.2) belongs to the Grandhaven cyclothem which succeeds the Dover cyclothem in the stratigraphic column.

The fauna collected at the following localities, Dover P-1, P-2, P-3, came from a generally dark gray to black argillaceous shale containing minor amounts of detrital quartz. The shales at these localities corre-

[2] For index numbers, see Moore, 1935: 22, p. 23, fig. 2; pp. 24–25.

Dry C-3.—

Bed Number		Thickness (In Feet)
5	Black, shaly soil bank, no fossils	1.7
4	Massive clastic limestone, of same lithology and fossils as Bed No. 5, Loc. Dry C-1	1.9
3	Dark gray argillaceous shale (Dry shale) containing about 2% spherical or flat and smooth, dark reddish brown-to-yellow, limonitic pellets or crusts 1–¼ mm., minor quantities of: coal fragments, calcareous shell fragments, detrital sandstone, detrital chert showing zooecia indicating silicious replacement of a bryozoan, broken iron-stained ostracod valves. The following specimens of the Dry shale limonitic fauna were found: *Imitoceras grahamense, Goniloboceras goniolobum, Crurithyris planoconvexa, Anthraconeilopsis kansana, Kansana discoidalia, Euphemitella emrichi, Straparolus (Euomphalus)? gladfelteri*	0.1–0.3
2	Light gray argillaceous shale with high calcareous content due to unidentified calcareous shell fragments, minor amounts of coal fragments	1.0
1	Thin banded coal, etc. same as Bed No. 2, Dry C-1	0.4
	Total Thickness	5.1–5.3

spond to the shale partings between the uppermost and middle Dover limestone members. In contrast, the fauna from localities Dry E-1 and E-1a came from a distinctly sandy-to-silty argillaceous shale that corresponds to Index number .8–.9 of the Dover cyclothem. At a higher horizon (Dry E-2), gray argillaceous shale was encountered. This shale contained a predominantly ostracod fauna. With the exception of some pelecypods found in lower beds, all other members of the Dry shale fauna appear to be absent. This bed may still represent lower Dry shale or may be the Grandhaven shale. In Elk County (localities Dry C-1, C-2, C-3) still higher beds of the Dry shale formation are found. These correspond to part of the Grandhaven cyclothem.

The two sections measured by the writer (Dry C-1, Dry C-3) can be compared to the ideal Wabaunsee cyclothem. At Dry C-1, the bed below the coal is a siltstone containing marine? fossils. This differs from the ideal member of Index number .1-ab (shale, sandy-to-clayey, a continental phase). Samples from the overlying very thin banded coal bed appear under the binocular microscope to incorporate an argillaceous and silty microfacies. The latter may correspond to Index number .1-ab. Beds corresponding to the cyclothem member of Index number .2 (clayey shale with *Myalina, Derbya, Chonetes*, etc.) vary at the two localities studied. At Dry C-1, immediately above the coal, we first encounter a more argillaceous, fossiliferous siltstone and then pass up into the usual *Myalina*-productid beds which are more calcareous. At Dry C-3 the bed immediately over the coal is a gray argillaceous shale with the usual calcareous fauna of this member in the ideal Wabaunsee cyclothem. However, the next overlying bed is a few inches thick and consists of dark gray-to-black argillaceous shale containing the typical limonitic fauna of the Dry shale.

The paleoecologic significance of these differences in fauna and lithology in beds immediately above the coal and below the limestone member (Index number .3) of the Grandhaven cyclothem, is taken up elsewhere in this study (p. 383 ff).

At locality Dry C-2 it is possible that beds tentatively assigned to the Dry shale correspond to the Dover limestone shale member (Index number .6) occurring as it does, between two limestone beds. There are other possible interpretations. For example, south of the Cottonwood River (Lyon County), the Dry shale is reported to contain a thin limestone stringer. In this limestone *Chonetes* and *Derbya* are abundant and other brachiopods, bryozoans, and crinoids are present. The stringer occurs about six feet above the so-called normal algal-fusulinid phase of the Dover limestone and is a very persistent bed (O'Connor, personal communication, 1951). A similar bed was observed by the writer at locality Dry C-1, Bed No. 4, although no information was obtained as to its regional persistence.

Coal fragments were found disseminated in the shale partings of the Dover and in the Lyon County exposures directly over the Dover limestone as well as in Elk County exposures of the upper Dry shale. Only at locality Dry C-1 are the coal fragments in the siltstone directly over the coal bed of

obvious origin. No coal beds have been reported from the Dover limestone formation or from northern exposures of the Dry shale. The persistent Nyman coal horizon of the Langdon shale (Moore, et al., 1951: 59) may have contributed the coal fragments found in the Dover shale partings. However, unless interfingering relationships exist between the Dry shale and the Dover limestone, it is unlikely that this could also have been the source of the coal fragments found in the Dry shale. By an alternative view, the source of the coal fragments of the Dry shale may have been very local and very thin coal beds occurring within the lower 6′ of the Dry shale in some Lyon County localities. No such beds have yet been reported and none were found by the writer, yet the possibility still remains.

Very limited published information on measured sections of the Dry shale is available. Of the three published sections (Moore and Moss, in Moore, 1937: 48, 52, 55) two are in Lyon and one in Shawnee County, Kansas. At these localities the formation is generally gray and clayey. At Shawnee, calcareous nodules presumably from the underlying nodular Dover limestone member are reported at the base of the Dry shale. No fossils were reported from the formation at any of these localities. Thickness at Lyon County localities is 10 feet. In the vicinity of Emporia golf course (O'Connor, op. cit.) it is approximately 8′ while at the Shawnee locality, it is 3.5 feet.

Generally, the lithology of the formation is that of gray argillaceous shale. In places, red and green shales have been reported. Sandy shale occurs locally. In Elk County there are thin coal beds. Over the coal two distinct faunas to which reference has already been made were found.

THE "DRY SHALE FAUNA"

The "Dry shale fauna" described here is not confined to that formation. The limonitic fauna described under "Systematic Paleontology" ranges from the shale partings of the Dover limestone through the Dry shale and possibly through the Grandhaven shale. Nevertheless, the name "Dry shale fauna" is retained because wherever its components occur, they are similar in size, composition, and enclosing rock material to that characteristic of the Dry shale.

While the "normal" calcareous fauna of the Dry shale is helpful to elucidate the paleoecology, it has not been systematically studied in the present paper since most of these species have been thoroughly investigated by students of the Pennsylvanian.

The only components of the "Dry shale fauna" specifically identified heretofore include two ammonoids, *Imitoceras grahamense* and *Goniloboceras goniolobum* (Elias, 1936, 1938, personal communication 1952; Miller and Downs, 1950). Some confusion has arisen because past collections were made in the then undifferentiated Emporia limestone in the vicinity of Emporia, Kansas, of which the present Dry shale represents a part. Thus Smith (1929: 63–80) had listed *Marathonites* and *Neodimorphoceras* as having been found at this locality and *Wiedeyoceras* has also been assigned to the Dover shale partings near Piedmont, Kansas. Part of the confusion has been clarified by Elias (1933) who noted that "Smith did not collect his 'Emporia' material himself. Perhaps he received a collection of true Emporia ammonoids mixed with other ammonoids from some other locality." At any rate, Elias (idem) was unable to recognize either *Marathonites* or *Neodimorphoceras* in the collections he studied.

Evidence of the present study makes it clear that neither of these genera were present in any of this material, Furthermore, based on Miller's description of the genus *Wiedeyoceras* a distinction cannot be made between the juveniles of *Goniloboceras goniolobum* and those of *Wiedeyoceras*. Only mature individuals show the distinctive generic feature, "with the exception of the ventral lobe, all of the primary lobes and saddles are rounded and undivided." This fact is emphasized by the need to place the following species of *Wiedeyoceras*, *pingue* and *nodomarginatum* under the synonymy of *Goniloboceras goniolobum* (see Miller and Downs, 1950: 197). Since the ammonoids belonging to *G. goniolobum* from the Dover shale partings and from the Dry shale were all juveniles, it becomes clear that the presence of members of the genus *Wiedeyoceras* cannot be demonstrated from the material at hand.

Beede and Rogers (1908: 233, 346) also designated some fossils belonging to the then undifferentiated Emporia limestone. These, however, cannot be specifically related to the Dry shale as presently defined. With the exception of the two cephalopods, none of the "Dry shale fauna" is included. Smith (Elias, personal communication, 1952) apparently recognized the presence of *Ambocoelia* (= *Crurithyris*) and *Leda* (= *Nuculana*) in what Moore has identified as being the Grandhaven shale. However, he was uncertain as to the assignment of the specimens and did not contribute any information about their specific identification.

The limonitic fauna of the "Dry shale" as determined to the present time is listed below. Three separate columns are used to indicate specimens obtained from the Dover shale partings (A), the Dry shale proper (B), and the Grandhaven shale (C). Species previously identified are shown by a single asterisk. Species previously identified elsewhere but not reported from any of the above subdivisions have a double asterisk. The question mark indicates probable occurrence as reported by Wooster and by Smith (Elias, op. cit.)

	(A)	(B)	(C)
CEPHALOPODA			
**Imitoceras grahamense* (Plummer and Scott)	X	X	?
**Goniologoboceras goniolobum* (Meek)	X	X	?
BRACHIOPODA			
**Crurithyris planoconvexa* (Shumard)	X	X	?
PELECYPODA			
**Nuculana bellistriata* (Stevens)	X	X	?
Anthraconeilopsis kansana Tasch, n. gen., n. sp.	X	X	X
Pleurophorus? dryensis Tasch, n. sp.	X	X	
Schizodus piedmontensis Tasch, n. sp.	X	X	
Aviculopecten sp. undet. I	X		
Aviculopecten sp. undet. II		X	
Nuculanella piedmontia Tasch, n. gen., n. sp.	X		X
Pleurophorus pseudoblongus Tasch, n. sp.	X	X	
GASTROPODA			
Kansana discoidalia Tasch, n. gen., n. sp.	X	X	
Strobeus cf. *paludinaeformis* (Hall)	X		
Euphemitella emrichi Tasch, n. gen., n. sp.	X	X	
Straparolus (*Euomphalus*)? *gladfelteri* Tasch, n. sp.	X	X	
Bellerophon wabaunseensis Tasch, n. sp.	X	X	
OSTRACODA			
***Hollinella gibbosa* Kellett			X
Hollinella dissimilis Tasch, n. sp.			X
***Bairdia beedei* Ulrich and Bassler			X
***Bairdia subconvexa* Coryell and Billings			X
Neobeyrichiopsis emporiensis Tasch, n. gen., n. sp.			X

Mineralogical composition of the fossils.— Most of the specimens were limonitic. These were dull, light rust brown, or dark iron brown with a submetallic lustre, or shades of brown intermediate between these two and either dull or of submetallic lustre. Most of the ostracods were calcareous and white or stained by iron oxide. A few ostracods were limonitic. One specimen, poorly preserved but probably assignable to *Goniologoboceras goniolobum*, was composed of chert. This specimen was found at locality Dry E-1.

As noted earlier, detrital chert occurs at several localities in minor quantities. Indications are that siliceous replacement was a minor and local event. It probably originated during the time represented by the upper limestone member of the Dover.

Calcareous and limonitic or calcareous-limonitic specimens of the same species occurred infrequently at different localities. A handful of the latter type occur in a sample of 859 specimens of *Crurithyris planoconvexa* at locality Dover P-3. A completely calcareous specimen, together with a limonitic internal mold of the gastropod *Euphemitella emrichi* were found at locality Dry C-2.

A calcareous test and limonitic mold of almost identical size of the ostracod *Hollinella dissimilis* occurred together at locality Dry C-3. Most specimens of ostracod species, however, were represented by iron-oxide stained valves.

FACTORS AND PROCEDURES INVOLVED IN ESTABLISHING CRITERIA FOR THE STUDY OF DWARFED MARINE INVERTEBRATES

Consideration of the following factors and use of the indicated procedures taken together provide an outline of a systematic procedure for the study of dwarfism not previously available in the literature.

1. *Composition of the fauna.*—The term "fauna" is a masking generalization. To establish the occurrence or non-occurrence of dwarfism, a fauna must be studied on the basis of individual components, i.e., ammonoids, brachiopods, pelecypods, etc. All statements to the effect that an entire fauna is less than two millimeters (Loomis, 1903) or is "diminutive" (Stauffer, 1937), etc., are considered invalid insofar as dwarfism is to be determined.

2. *Composition of the individual components of a fauna.*—The number of specimens of any species in collections from the "Dry shale fauna" varies from single individuals to upward of a thousand. These are to be viewed as samples of an enormously larger population.

3. *Nature of preservation.*—For growth stage determination, there is a minimum required preservation. Thus, specimens of *Imitoceras grahamense* so badly weathered that no sutures were visible, could not be used for the purposes of the present study.

4. *Size distribution within segments of a population.*—After the fauna was separated into species, all specimens of a given species were measured. Where part of a specimen was broken off at a place involving one of the critical dimensions, such dimension was estimated and the measurement recorded with a question mark following it. The degree of error attached to such estimates is slight when like measurements for unbroken specimens are compared. All measurements were entered in a notebook under proper column headings alongside of an identifying number for each specimen. Measurements for specimens of the same species but different collecting localities were entered under the locality designation. (For a complete tabulation of measurements, see Footnote 1.)

Measurements of holotypes and other types, while providing useful data, are, in themselves, inadequate for determination of dwarfism. The whole sample available to an investigator should be used as a basis for approximation of size variation within a given species.

5. *Graphic analysis of size distribution.*—Following the procedures effectively employed by Percival (1944), Spjeldnaes (1951), Kesling (1951), and others, curves were plotted for length and width or for the largest dimensions, such as maximum diameter, for all species represented by an adequate sample. Interpretation of these curves followed the usual procedures (Simpson and Roe, 1939). In addition to graphic analysis, *all other evidence* was called upon before a conclusion was reached as to the growth stage or stages represented in a sample. Such evidence included, for example, morphologic criteria, size grade analysis of the entire fauna, etc.

6. *Morphologic criteria for determination of growth stages.*—Such criteria will, of course, vary for different components of a fauna. Relevant data of this type previously established and used by other workers are considered in the next section in relation to the particular problem being studied. (See, for example, the discussion of *Strobeus* cf. *paludinaeformis.*)

7. *Available data on size distribution.*—Although little systematic attention has been paid to this aspect of the problem, many published papers on fossil faunas do contain numerical size data. Data on the size distribution of a given species or genus occurring on the same, lower or higher levels, at nearby or widely separated localities, can have important bearing on determination of growth stages in a given sample. Such data can have a further value, providing the investigator with an approximate upper size limit for a given species or genus. This, in turn, may prove to be a critical consideration in determining whether one or more components of a given fauna are dwarfed. (See, for example, table 4.)

8. *Growth stages and dwarfism.*—To report with any degree of confidence that a given sample consists of specimens representing either juvenile and/or adult growth stages, it is desirable to include information of the type discussed under items 4, 5, 6, 7, although this may not be available in every instance.

Determination of growth stages is only a preliminary step. *Dwarfism of components of a fauna cannot be demonstrated unless it can first be shown that we are dealing with adult growth stages.* There is much confusion in the literature on this subject. Richter (1913) thought that he had some dwarfed trilobites. A recent writer made reference to "dwarf trilobites" as well as other dwarfs among microfossils (Ellison, 1951). Yet, in the Arthropoda, ecdysis will of necessity provide quantities of successive molts graded in size from very small to relatively large. If the procedures outlined are followed, such trilobite molts readily appear to the student as immature growth stages. Kellett's photographic sequences of ontogenetic stages of ostracods effectively illustrate this observation.

Another inadequate procedure is to compare the fauna above and below a given bed containing alleged "dwarfs" (Cumings and Beede, 1906; Fisher, 1951). While this procedure is noted under item 7 above, it cannot clarify the growth stages involved by itself. Information obtainable under items 4, 5, and 6 is a necessary preliminary. Similarly, employment of morphologic criteria alone or out of the context of the size distribution of the population sampled, does not allow for aberrations due to previously unrecognized causes (Wilson, 1951:17–18, and plate 1, fig. 1; Rothschild, 1935:537–546). Such aberrations may occur as stunted or giant forms due to such causes as deficiency diseases, bacterial infection, etc.

9. *Adult growth stages and dwarfed components of a fauna.*—When the adult specimens of a given component are isolated, the size range should be compared with (a) the size range for a sample of the same species known from other formations, and (b) with juveniles of the same species in the same beds. The results of such comparisons are in themselves inadequate unless placed in the context discussed in item 10.

10. *Size grade analysis of the entire fauna.*—A size grade analysis of an entire fauna, as it is represented in a given collection regardless of species, can readily be made based on maximum diameter. These data are provided under item 4. When used in conjunction with item 9, the investigator will have an additional indication as to whether the "small" adult specimens of a given sample are true dwarfs and whether or not their occurrence together with the rest of the fauna is a function of selective sorting by bottom currents.

11. *Paleoecology.*—Once either dwarfism or high infant mortality among a given group of marine invertebrate fossils is established, paleoecologic criteria will then be most useful in exploring probable causes. It should be emphasized that paleoecologic criteria cannot establish, although it may help to confirm, the dwarf status of a given component of a fauna.

12. *Evidence of the biological sciences.*—By certain significant generalizations (Wimpenny, 1941; Hammett, 1934; Barnes, 1932) the essential findings of numerous documented biological studies are summarized. These are helpful in the study of factors that may have affected size variation in fossil marine invertebrates.

SYSTEMATIC STUDY OF THE "DRY SHALE FAUNA"

The systematic procedure outlined in the preceding section is applied to the study of each component of the "Dry shale fauna" in the discussion that follows.

Imitoceras grahamense.—Students of ammonoids (Miller, Elias, Plummer and Scott, et al.) accept the following morphologic criterion of growth stage: the closer spacing of sutures adorally and especially the crowding of the adoral sutures indicate maturity (cf. Miller, 1947:18; Miller and Downs, 1950:194). In the past "having less crowded septa in late maturity" was considered to be a specific difference between *Goniloboceras welleri* and *Goniloboceras goniolobum* (Elias, 1938:96–97). *G. welleri* has, however, since been placed under the synonomy of *G. goniolobum* (Miller and Downs, idem). Any such differences must be related to growth stages within a species.

Of 206 usable specimens of *I. grahamense*,

30 were found to be mature when the above criterion was used. Each of these mature forms had four or more (to 21) external sutures well preserved. The distances between the apices of the first ventrolateral saddle of each pair of sutures of the 30 mature forms, starting with the most adoral suture, was measured under the binocular microscope. A table of distances between successive pairs of sutures was thus compiled for 16 specimens. In addition, for comparative purposes, similar measurements were made on three juvenile specimens and two specimens of the same species from the Wayland shale. Table 1 gives the results.

Table 1 reads from left to right as follows: for the first specimen, with a maximum diameter of 7.9 mm, the distance between the most adoral suture and the next suture before it is .250 mm, between the latter suture and the next suture before it, .275 mm, etc. The distance between the apices of the first ventro-lateral saddle of any two sutures was chosen arbitrarily because it was clearly preserved on most adult specimens.

The first question we must ask is, "What may be the meaning of a difference in spacing between successive pairs of sutures?" The mode of growth of the living animal was to evacuate successive areas of the shell and to secrete a wall at the rear of its living chamber. Such camerae are thought to have been filled with a nitrogenous gas and to be an adaptation for buoyancy (Dunbar, 1924; Miller, 1947:18–19). The distance between any two such septal walls cannot, of course, be given by a single measurement of distance between similar parts on two successive sutures. Nevertheless, a measurement of this type is indicative of probable gross differences in suture spacing for a given conch. Clearly, a similar measurement in different parts of a suture would give different readings.

If we take any given specimen from Table 1, for example, one with a maximum diameter of 4.2 mm., it will be noted that the growth of the animal apparently was being retarded in the later stages of growth. Aberration in the amount of decrease between successive pairs of sutures may be related

TABLE 1.—DISTANCE BETWEEN APICES OF THE FIRST VENTRO-LATERAL SADDLE OF SUCCESSIVE PAIRS OF SUTURES IN ADULT FORMS OF *Imitoceras grahamense*

Maximum Diameter of Specimen (mm.)	Most Adoral Suture	Distances between Successive Pairs of External Sutures Visible without Breaking Back the Shell (mm.)									
7.9	.250	.275	.287	.350							
7.7	.525	.575	.500	.475	.500	.625*					
6.8	.400	.325	.400	.375	.400	.225	.250	.250	.225*		
6.4	.150	.312	.275	.250	.175	.175	.225				
6.4	.175	.150	.200	.350							
6.0	.175	.200	.225	.175							
6.0	.125	.250	.262	.275	.450	.300	.250	.325	.275	.275	
		.250	.375								
5.8	.125	.200	.275								
5.8	.150	.225	.312	.200	.287	.450					
5.5	.200	.275	.350	.500	.325	.550					
5.5	.250	.225	.175	.325	.300	.325**					
5.2	.050	.175	.200	.125	.175	.125					
4.9	.225	.225	.225	.275	.325	.375	.400				
4.5	.200	.275	.175	.250**							
4.2	.175	.275	.125	.225	.225	.175	.300	.275	.225	.200	.225
		.250	.275	.450	.350	.325					
4.1	.200	.175	.200	.100	.225	.275	.350				
4.0	.225	.175	.225	.250	.300	.275	.250	.275			
4.0	.275	.375	.250	.225	.275	.250**					
3.4	.175	.325	.425	.575	.525	.725	.450	.250	.275	.225	

* Wayland shale specimens of the same species (S.U.I. 3299).
** Dry shale juveniles of the same species from the Dover shale partings near Piedmont, Kansas.

to the need for volumetric adjustment of cameral spacing to satisfy the demands of buoyancy. According to Miller (1947, idem), each septum probably corresponds to a period of repose.

Reference to Table 1 will indicate that for the specimen with a maximum diameter of 7.9 mm. there was a steady decrease in distance between sutures for all sutures observed. It would seem to be quite possible to have a progressive decrease in spacing and then a repetition of a given distance two or three or more times. This may be viewed as a variation of the retardation type of slowdown in growth mentioned above. Another type may combine greater spacing intervals together with a prolonged slowing down. A specimen from the Wayland shale shows this condition. (See Table 1, specimen with maximum diameter of 6.8 mm.) The Wayland shale specimen was figured as a "mature" specimen (Miller and Downs, 1950, S.U.I. 3299, pl. 32, figs. 1–4). In the later stages it is "slowing down." Yet it shows sufficient increase over the older stages of growth in the later suture spacings to place it more as a late adolescent than an adult. The size of the specimen (diameter, 6.8 mm.) in itself cannot be used as an age criterion since 13 specimens from the Dover shale partings of diameters 6.0–8.9 mm. were found to be juveniles based on suture spacing.

Entries for juveniles included in Table 1 may be viewed in the same manner as indicated above. Any spacing between older septa may be equaled by the spacing of the youngest septa. This relationship does not hold for adult specimens. For adults the rule appears to be a decrease in distance between the most adoral sutures as compared to the distance between the older septa. Thus, rather than relying on the qualitative expression "closer spacing" for the most adoral sutures as a criterion of maturity, the above table and discussion suggest that a quantitative statement permitting comparisons between suture spacings in the same and in different specimens, is possible.

After the growth stages represented in the sample have been established and the adults have been segregated, the next question that arises is, "Are these adults dwarfed?" A most direct way to answer this question is to graph the maximum diameters for all adult and all juvenile specimens separately (figure 1).

If it can be shown that the size range of proven adults approximates that of the juveniles, this will demonstrate that with continued growth the juveniles would have reached (i.e., had they survived they were potentially capable of attaining) sizes greater than that for the largest known adult in the group. This would be evidence in favor of dwarfism. However, additional types of evidence will then need to be employed to check on this conclusion.

Reference to figure 1 shows that the size range of the adult imitoceratids are within the size range of the juvenile imitoceratids. As already noted, this suggests that the adults are dwarfed. How, then, does the mean diameter of the adults of this species vary in time? In the presumably older Dover shale partings in southern Kansas, the mean diameter of imitoceratid adults is 4.93 mm., while in the younger beds (the lower portion of the Dry shale—Emporia) the mean diameter is 5.89. Using standard statistical procedures, we obtain $d/\sigma = 2.52$. This figure is usually significant (Simpson and Roe, 1939, p. 191). It is interpreted to mean that the difference in mean diameter at Piedmont and at Emporia is one that most likely did not arise by chance.

If the conclusion is accepted that the adult imitoceratids were dwarfed, then the above result signifies that the mean diameter of dwarfed adults during the time repre-

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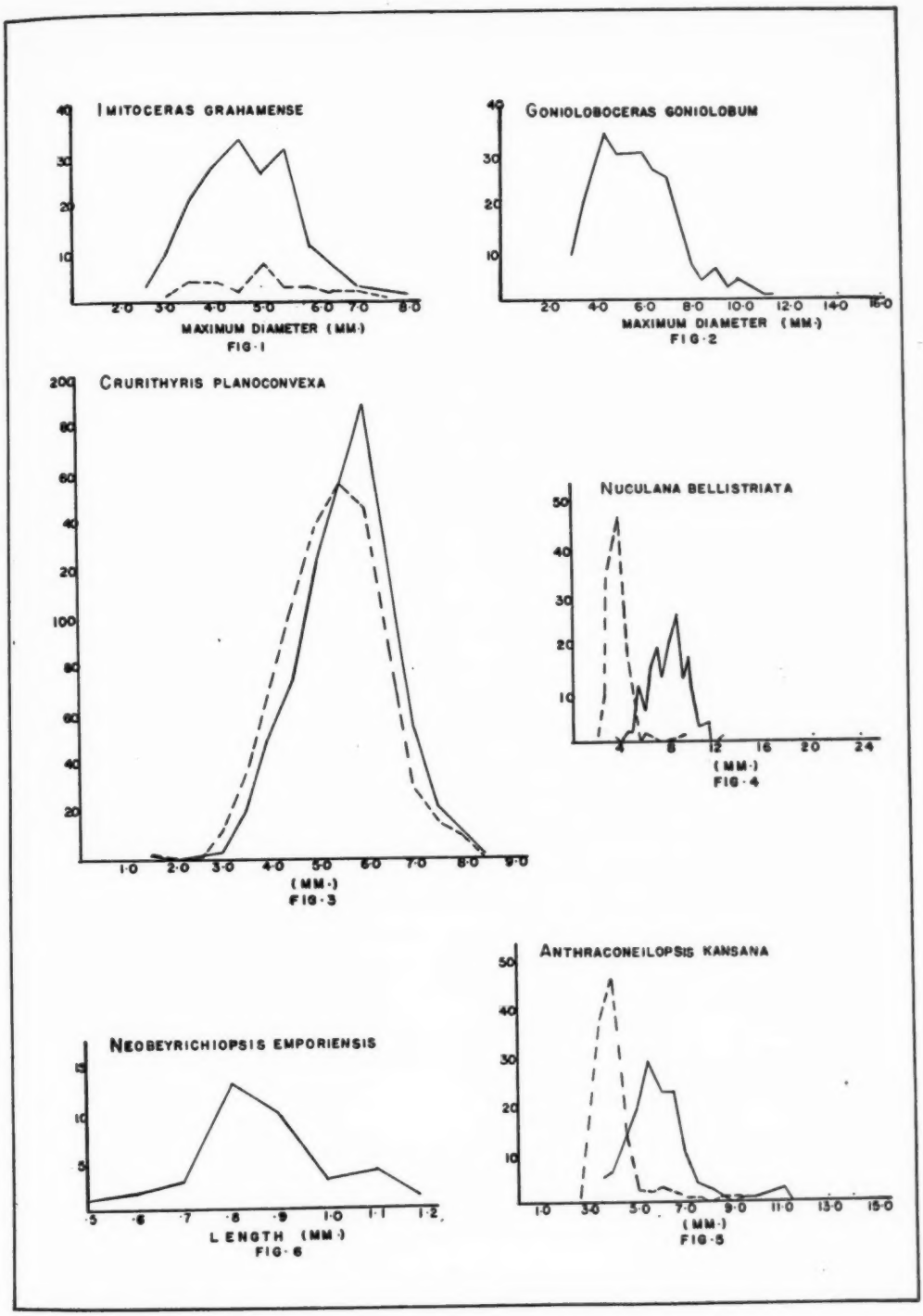
EXPLANATION OF TEXT FIGS. 1–6

FIG. *1*—*Imitoceras grahamense*, solid line indicates juveniles only; dashed line, adults only.
2—*Goniolobоceras goniolobum*, solid line indicates juveniles only.
3—*Crurithyris planoconvexa*, solid line indicates width; dashed line, length.
4—*Nuculana bellistriata*, solid line indicates length; dashed line, width.
5—*Anthraconeilopsis kansana*, solid line indicates length; dashed line, height.
6—*Neobeyrichiopsis emporiensis*, solid line indicates length.



For Figs. 1–6, ordinates show number of fossil individuals.

sented by the Dover shale partings, was smaller than the mean diameter of dwarfed adults during the time represented by the lower portion of the Dry shale. In other words, within the general framework of dwarfism, a size increase occurred in time. This is rather interesting since a size decrease in time has been noted for the genus *Imitoceras* in general. Thus, Upper Devonian and Lower Mississippian imitoceratids attain a much larger size than the Pennsylvanian and Permian representatives of the genus (Miller and Unklesbay, 1943; Miller and Owen, 1939; Miller and Downs, 1950). Three specimens of *I. pygmaeum* (Gemmellaro) from the Permian Sosio beds of Sicily had diameters of 6.9, 8.7, and 11.0 mm. respectively (cf. Gemmellaro, 1888:39; Miller, 1933:420–421). These specimens were made available by Professor A. K. Miller and measured by the writer. While an upper limit for the diameter of Pennsylvanian to Permian forms is 12 mm., forms like "*I. discoidale*" from the Mississippian (Miller and Collinson, 1951) reach diameters to 45 mm., and such European forms as *I. gurichi*, *I. intermedium*, *I. acutum*, and *I. denckmanni* from the Upper Devonian attain maximum diameters of at least 75 mm. (Schindewolf, 1923:325–339; A. K. Miller, personal communication, 1952).

The suggestion has been made that possibly Pennsylvanian and Permian forms of this genus "are degenerate representatives of an entirely different stock or stocks and therefore generically distinct from the typical *Imitoceras*" (Miller and Downs, 1950). Plummer and Scott proposed that such forms (Pennsylvanian) be incorporated under the genus *Neoaganides*. The suggestion of Miller and Downs is one possibility. Another one might be that we are dealing with essentially the same stock or stocks from Upper Devonian to Permian but that this is a unique example of a generic size decrease which contrasts interestingly with what appears to have been a major evolutionary trend among marine invertebrates (cf. Newell, 1949).

Placing the "Dry shale" adult imitoceratids in the context of a generic size decrease in time, it becomes obvious that the mean adult diameter is well below the upper size limit for Pennsylvanian imitoceratids in general. This observation would appear to support the interpretation that the "Dry shale" adult imitoceratids may be true dwarfs.

In accordance with criterion 10, we still have to place the size distribution of *Imitoceras grahamense* in context of the size distribution for the fauna as a whole as represented in the collections at hand, irrespective of species. This is given in Table 2.

Table 7 indicating size grade distribution of the entire fauna regardless of species, shows that the major grade size of the above sample for juveniles and adults is the same as that for the entire "Dry shale fauna," i.e., small pebble size. This can be interpreted to mean that if dwarfing did occur, it probably did not take place at the site of final deposition. Dwarfing could have presented the available bottom currents with a size grade within its general competence and thus movement from an original site of deposition in bottom mud would be facilitated.

Conclusion: Based on the criterion "closer suture spacing adorally denotes maturity," some specimens of *Imitoceras grahamense* appear to be mature. These adult specimens fall within the size distribution for juveniles of the same species and same sample. They are thus interpreted to be dwarfed.

TABLE 2.—SIZE GRADE ANALYSIS OF *Imitoceras grahamense*

Grade Limits Diameter in Millimeters	Name	Dover Shale Partings		Dry Shale	
		(Juvenile) Per cent	(Adult) Per cent	(Juvenile) Per cent	(Adult) Per cent
16–8	Medium pebble		1.0		
8–4	Small pebble	91.4	78.2	90.0	89.5
4–2	Granule	8.6	20.8	10.0	10.5

Goniloboceras goniolobum.—Elias (1938: 98–99) recognized two immature and one mature stage of development in this species. These stages were glyphioceran, milleroceran, and goniloboceran. The milleroceran stage is defined as being characterized by "its inflated conch nearly elliptical in cross section (platycone) and its suture with angular and pointed lateral lobes and subangular and non-pointed lateral saddles." The milleroceran stage changes into the mature goniloboceran stage when the first lateral saddle becomes pointed upon attaining a diameter of about 18 mm.

Based on this definition, it is possible to separate juvenile stages from adult stages without reference to comparative spacing of the most adoral suture. Elias found that of all the specimens of this species that he had studied from the Dover shale partings and the Grandhaven shale, the genus "is represented exclusively by juvenile individuals of glyphioceran and rarely milleroceran stages of development." Miller and Downs (1950:198) defined a mature suture. These two definitions form the basis for separating out growth stages in the present collection.

Out of a total usable sample of 175 limonitic internal molds, all 175 are classifiable as juveniles. This finding confirms the observation made by Elias. The juveniles may be subdivided into glyphioceran stage with 167 specimens, and milleroceran stage with eight specimens. The subdivision of juveniles is supported by study of sutures for the glyphioceran stage. Poorer preservation in many cases required reliance on graphic analysis for recognition of the milleroceran stage. This analysis indicated that for all specimens in the class above 10.9 mm., a later juvenile growth stage than for the rest of the sample is to be assigned. (fig. 2).

Table 3 shows that a size grade analysis for the sample of this species regardless of locality falls into small pebble size as the major grade size. This result conforms to the findings for *Imitoceras grahamense* and for the fauna as a whole.

What appears to be a complete absence of goniloboceratid adults in the "Dry shale fauna" is puzzling and requires further consideration. Elias (personal communication, 1952) refers to the occurrence "of a fragment of nearly adult *Goniloboceras*" in the same zone as juveniles of this species. This specimen was seen in the collection of the late Professor Wooster of Emporia College. Most probably this fragment is not larger than small pebble size.

TABLE 3.—SIZE GRADE ANALYSIS OF *Goniloboceras goniolobum*

Grade Limits Diameter in Millimeters	Name	Dover Shale Partings (Juvenile) Per cent	Dry Shale (Juvenile) Per cent
16–8	Medium pebble	7.3	13.8
8–4	Small pebble	80.2	77.1
4–2	Granule	12.5	9.1

Adults of the species are known to range from 32–16 mm. (Elias, idem) large pebble size, to about 100 mm. (Miller and Downs, op. cit.) small cobble size.

A reconstruction of probable events would seem to be somewhat as follows: juvenile stages would seasonally become the dominant element of the population. In samples of living marine invertebrates taken at varying depths, it is quite common to find 50% or more in any sample that are juveniles of certain species [Foraminifera, Phleger, 1951; brachiopods, Percival, 1944; copepods, Gunter, et al, 1948; ostracods, Kesling, 1951; cf. fossil ostracods, Spjeldnaes, 1951; gastropods (*Busycon carica*), Magalhaes, 1948, pp. 390, 406; pelecypods, Ford, 1925, p. 534, table 1]. In this connection, it is important to note that the frequency of different growth stages occurring in hauls made at different seasons of the year will vary. Thus, for the euphausiids *Thyanoessa* and *Meganyctiphanes*, May tows in the Bay of Fundy showed a 300% increase in the number of juveniles as compared to previous months (Fish and Johnson, in Whitely, 1948: 251). Further, a September tow on Georges Bank may consist dominantly of juveniles while in the following May the September brood will have reached maturity and adult stages will dominate in tows (Whitely, idem: 235–263, p. 252, table 2). At death, the gas-filled

chambers of juvenile and adult goniolobo-ceratids would, while intact, support the the shell in water. When the gas escaped the shells would settle on the sea bottom. Once on the bottom and either before or after formation of the limonitic molds, currents would move by traction through the turbid water above the unconsolidated clayey and silty mud, those goniolobo-ceratids ranging in size from granule to medium pebble. That is to say, *juveniles only, or fragments of adults within this size range* would be moved. Accompanying turbulence would probably move the surficial silty clay on the bottom as well, but this would be in addition to the movement of the larger detritus.

Evidence for such movement of limonitic molds and related events on the sea floor may be found in the specimens. Most specimens show the effects of abrasion, fragmentation of internal molds and rounding of fragments; distortion of internal molds by compaction and other stresses and subsequent smoothing and rounding; sediment deposition in the living chamber, occasionally swelling and cracking of some internal molds and subsequent wearing down of this sediment-filled chamber until in many instances it approached the external curvature of the penultimate whorl.

Using the multiple hypothesis approach, one may explain the absence of any internal molds of adult goniolobo-ceratids. Thus, we may postulate three alternatives:

1. *Adult goniolobo-ceratids are represented in the present material but only the inner whorls (juvenile stages) remain.* This seems unlikely in view of the fact that some of the largest specimens have almost all the external sutures preserved, the most adoral of which do not have angular saddles or lobes which characterize the "adult."

2. *Adult goniolobo-ceratids would be found if a larger sample were available.* This also seems unlikely since the present material includes extensive collections made by the the writer in addition to several other investigators at different times and at different localities. An earlier investigator, Elias, as already noted, also reported the absence of adult goniolobo-ceratids.

3. *The absence of adults is a dual result of* (a) *high seasonal mortality of numerous young at periods when they were the dominant element of the population,* and (b) *incompetence of current sorting on the bottom to move grade sizes larger than medium pebble size, i.e., adult goniolobo-ceratids.*

Based on all the evidence, hypothesis 3 seems most likely.

Juvenile stages of *G. goniolobum* seem to predominate in the various horizons from which they have been reported. The shale beds of the Abo sandstone formation of south central Texas contain species of several genera (*Milleroceras, Gurleyoceras, Wiedeyoceras*) that have been reassigned to *G. goniolobum* (Miller, 1932: 59–93; Miller and Downs, op. cit., 196–200). A review of the goniolobo-ceratids mentioned above indicates the predominance of specimens representing juvenile stages with maximum diameters ranging from 6–12 mm. Relatively few of these goniolobo-ceratids were of larger dimensions (*Milleroceras parrishi*, 17 mm.; *Gurleyoceras discoidale*, 25 mm.). *G. welleri* has been reassigned to *G. goniolobum* (Miller and Downs, idem) and only young individuals occur in large concretions in the shale overlying the Elmo coal in Nodaway County, Missouri (Elias, 1938: 97). *G. welleri* also occurs in great abundance in the Wayland shale of the Graham formation, and Cisco group in Graham, Texas. The museum collections of the State University of Iowa indicate an abundance of juvenile stages represented in the small limonitic molds. Elias (idem) figured and described a few mature specimens from the Wayland shale, but all indications are that juvenile stages were the dominant element in the population.

Similarly, *G. goniolobum* was found to be the most abundant species in the Finis shale of Texas where apparently juvenile forms were dominant (Miller and Downs, idem).

This widespread predominance of juvenile stages of *G. goniolobum* in different areas [Kansas, Missouri, Texas, Oklahoma (Nelly Bly formation)] covered by the Pennsylvanian seas at varying times, suggests a recurrent high seasonal mortality of the young. Second, having a maximum diameter compatible with the competence of prevailing bottom currents to move by traction, the identity of this goniolobo-ceratid necrocoenosis was not disturbed by transport.

The fact that many of these formations yield goniolobocerati ds represented by limonitic internal molds, raises the question as to whether iron-rich or sulphate-rich waters may have contributed to the postulated recurrent high seasonal mortality of the young. This question will be discussed in more detail under "Paleoecology."

Conclusion: The entire sample of *Goniolobocerαs goniolobum* of the "Dry shale fauna" represents only juvenile stages.

Crurithyris planoconvexa.—Two major criteria were used to determine the growth stages represented by the large sample of this brachiopod. These were graphic analysis and comparison with reported size distributions of this species elsewhere in Pennsylvanian beds. The graphic analysis duplicated the procedure used by Percival for living *Terebratella* (1944). Intervals of 0.5 mm. were used. Separate curves for length and breadth of specimens were plotted (figure 3).

More than 50% of the total sample of 859 specimens fall in the range 4.5 mm.–6.5 mm. The curves obtained are single-peaked. They show no discontinuities except minor ones at the lowest part of the size range. These curves contrast strikingly with those obtained by Percival for a sample of 711 specimens of *Terebratella inconspicua.* Percival's curves show a series of secondary peaks which he interpreted as denoting four distinct year classes or growth stages. The results obtained with *Crurithyris planoconvexa* are most compatible with the part of Percival's curves designated "First year class" or youngest juvenile stage represented in that sample. The logical interpretation of these curves is that there is only one (or possibly two) juvenile stage represented. However, we need not rely solely on graphic interpretation.

Dunbar and Condra (1932: 346) gave a length of 8.0 mm. and a width of 8.5 mm. as "normal size in many of our lots." They noted also that there is a considerable variation in size from bed to bed and that in some localities shells of this species are decidedly smaller. Beede (1900: 101–102) gave a length of 9.0 mm. and a width of 10.0 mm. for *Crurithyris planoconvexa.* Thus, in both Nebraska and Kansas, the average size of specimens is, on the whole, distinctly larger than those of the "Dry shale fauna." However, this cannot be interpreted as due to dwarfism since the distribution of the "Dry shale" sample reaches a low culmination point precisely at 8.5 mm. This fact indicates, as does the nature of the distribution curves, that we are dealing with a predominantly juvenile sample with a smattering of adults present. Viewed in this way, we can explain the fact noted for the Nebraska specimens, namely, that in some localities shells considerably smaller than the "average" are dominant. At such localities we are dealing with juveniles. Where the "average" sized specimens occur in the Nebraska Pennsylvanian, the sample presumably is dominated by adult elements of the original population. This would hold for Beede's larger specimens as well.

It is of some importance that the larger shells (adults) are slightly larger than small pebble size while the bulk of the "Dry shale" sample falls within small pebble size. This grade size, as already noted, is the major grade size for the entire fauna of the available sample and as such, cannot be unrelated to selective bottom sorting.

The occurrence of a preponderance of juveniles among living brachiopods was also found by Percival in his study of *Terebratella inconspicua.*

Conclusion: The bulk of the specimens of *Crurithyris planoconvexa* in the "Dry shale fauna" represent juvenile growth stages. A few specimens represent undwarfed adults.

Nuculana bellistriata.—The major criteria for determination of the growth stages represented by samples of this pelecypod in the present collection are: first, graphic analysis; second, a tabulation of sizes for specimens of this species reported elsewhere is compiled and used as a frame of reference; third, the designations "adult" and "juvenile" given to specimens of this species which were studied by Girty (1903; 1915a, b) afford a specific reference point for comparative purposes.

Based on Girty's illustration of *Nuculana bellistriata,* it is possible to derive the critical dimensions by measuring the photographs given at natural size. Plate 14, figure 1 (1915b) shows a right valve of a char-

acteristic ["average" (?)] specimen of length equal to 19 mm. and height equal to 10 mm. Figure 7 of the same plate shows "a very young specimen's right valve" with length equal to 10 mm. and height equal to 5 mm. In other words, the "average" or what Girty considered to be adult-sized individuals, were approximately twice as long and twice as high as the early juveniles of the species.

A compilation is given in Table 4 of the sizes noted by different authors.

From this table, if we follow Girty, we may conclude that all the specimens of Sayre and Branson represent early juvenile stages; that the specimens of Stevens, Hall, White, and Beede were undoubtedly representatives of mature growth stages. Branson's Rex chert specimens are also in the mature group.

Based solely on the 161 specimens of the "Dry shale" and the curves for length and height obtained when the frequency of occurrence is plotted (figure 4), the following conclusions are drawn:

(a) That the distribution falls into two distinct age groups. The curve for length shows the bulk of the sample to fall in the range of from 4 mm. to 12 mm., while the curve for width indicates a range of from 2 mm. to approximately 5 mm. These two curves overlap and are taken to represent the juvenile age group. At 20 mm. and 24 mm. there are isolated points. These are interpreted as representing part of a second group, namely, adults.

(b) That the discontinuity between 20 mm. and 24 mm. is probably a function of a limited sample. Given a larger sample, we might assume that these isolated points would be the beginnings of or part of another peak which would spread beyond 24 mm.

While the above conclusions were reached solely by graphic analysis, it is possible to obtain confirmation by other means. Thus, reference to Table 4 indicates that Girty's juveniles fall within our main distribution curve for length and width. His adults correspondingly fall in the area of our isolated points. Similarly, the size of Sayre's average specimen would be close to the average size of the "Dry shale" juveniles. On the other hand, the specimens of Stevens, Hall, White, and Beede would fall in the area of our isolated points. Incorporating these

TABLE 4.—SIZES REPORTED BY AUTHORS FOR THE PELECYPOD *Nuculana bellistriata*

Author	Length (mm.)	Height (mm.)	Remarks of Author	Formation	Locality
Stevens (1858)	17.7	10.1		Roof of Danville Coal, etc.	Ohio
Hall (1858)	18.0	9.0	Smaller indiv.	Lower Coal Measures	Illinois
	21.0	12.0	Larger indiv.		
White (1883)	27.0	12.0	*	Coal Horizon	Indiana
Beede (1900)	27.0	14.0		Upper Coal Measures	Kansas
Girty (1915b)	19.0	10.0	Adults	Wewoka	Oklahoma
	10.0	5.0	Very early juv.		
Sayre (1930)	8.0	4.5	Average size	Drum limestone	Missouri and Kansas
Branson (1930)	(2.0–12.0)**		Average length, 5 mm.	Phosphoria	Montana, Wyoming
	25.0			Rex chert	Idaho

* This is the greatest length White observed. "A large majority of them are considerably smaller than this."

** The figures given indicate a range for length only.

dimensions into the present distribution would establish a distribution curve for adults ranging from 17 mm. to 27 mm. for length while a secondary peak would probably occcur in the range 9 mm. to 14 mm. for height. Curiously, the range in length of the Phosphoria specimens, 2 mm. to 12 mm. (Branson, op. cit.: 43) parallels the spread found in the bulk of the "Dry shale" sample and hence may be taken also to represent juvenile growth stages.

Apparently *Nuculana bellistriata* was the most abundant pelecypod species in the "Dry shale." Girty similarly found it to be exceedingly abundant in the Wewoka. Curiously, the Drum limestone oolitic member (Sayre, op. cit.) in the Kansas-Missouri area also contains abundant juveniles of this species. Although the growth stage attained was not one of Sayre's considerations in describing this species from the Drum, he made the pertinent observation (idem: 80–81):

> The Drum fauna of the type locality (along Drum Creek, just east of Independence, Kansas) is generally robust, while that of the Drum of the Kansas City area is *essentially a dwarf fauna* although some forms attain large size. Otherwise, the faunas of the two areas are similar with the exception of the gastropod elements which appear less abundant in the south. (Italics mine.)

The analysis of known size distribution of *N. bellistriata* in the "Dry shale fauna" and elsewhere given above makes it apparent that Sayre's specimens were not dwarfs at all but represented juvenile stages. It appears that two types of forms occurred in Sayre's dwarf fauna: those that attained large size and were not dwarfed, and others that although of small size, were also not dwarfed.

The relatively thin (6–20 feet) oolitic member of the Drum limestone in the Kansas City area (Sayre, idem: 79–80) contains the so-called "dwarf fauna." The thicker oolitic limestone of the type locality (about 80 feet thick) which is also quite fossiliferous, contains a so-called "generally robust" although not essentially a dwarf fauna. It has been pointed out (Moore, 1949: 97) that "fossils from various other oolitic limestones which were miscorrelated with the Drum, are included unfortunately, in the 'Drum' fauna." Hence, we are probably not dealing with the same fauna at the two localities mentioned above. However, a suggestion has been made that since oolites and dwarf fossils are often associated (Moore, 1929: 471–473; 1948: 126), there may be something in the formation of oolites that could explain dwarfism in such cases. The evidence of the present study indicates that this association could rather be explained in terms of selective bottom sorting *without recourse to dwarfing* to explain the small assemblage. The fact that so-called dwarf forms often occur in association with oolites, strengthens the general interpretation given in the present paper that sedimentary and not biological processes are responsible. (See Part II.)

On the other hand, as far as evidenced by *Nuculana bellistriata*, no dwarfism is indicated in the Drum of the Kansas City area. One further observation can be made about this so-called "dwarf fauna." Its occurrence is not adequately documented nor criteria for determination of "degree" of dwarfism given (cf. Gayle Scott, 1924: 12). Such criteria have not been established for any fauna or components of a fauna, fossil or living.

Conclusion: The specimens of *Nuculana bellistriata* of the "Dry shale fauna" represent juvenile growth stages with a few undwarfed adults present.

Anthraconeilopsis kansana.—Since this is a new genus and new species, the criterion for determination of growth stages is limited to graphic analysis. The total sample is represented by 145 specimens. Two curves, one for length and one for height, were obtained using an interval of 0.5 mm. These curves are interpreted as follows (fig. 5):

(a) The curve for length shows that the bulk of the sample is in the range 3.5 mm. to 9.0 mm. Within this range there are no discontinuities nor recurrence of peaks and the curves for length and height overlap. This is considered to denote juvenile growth stages.

(b) At 11 mm. a secondary peak occurs, thus indicating the presence of a few undwarfed adults.

(c) A discontinuity occurs between the intervals 11.5 mm. and 12.5 mm. The flatness of the curve in this part of the graph may be merely apparent and if more specimens were available, this might be found to

be the tail of the sector showing a secondary peak.

(d) Two major collecting localities are represented in this graph: Emporia and vicinity, and Piedmont and vicinity. Since no Emporia specimens attained sizes of 9 mm. or greater, it appears that at Emporia all specimens represent only juveniles. At Piedmont, then, both adults and juveniles were represented.

Conclusion: The specimens of *Anthraconeilopsis kansana* in the "Dry shale fauna" predominantly represent juvenile growth stages. A few undwarfed adults are also present.

Pleurophorus? dryensis.—Only three specimens were found in the present collection. From the marked curvature of the beaks, it is probable that these molds represent adult stages. However, the size of the sample is so small as to preclude determination of the mean size of the population. This is especially so since the three available specimens comprise a new species.

Conclusion: The specimens of *Pleurophorus? dryensis* in the "Dry shale fauna" may represent adult growth stages but this cannot be stated with certainty. If they represent adults, no conclusive evidence for or against dwarfism is available.

Schizodus piedmontensis.—Two criteria were used in determination of the growth stages: consideration of morphologic development and comparison with a closely related Chinese species. Graphic analysis proved inconclusive because of the small sample. Closely spaced concentric growth lines and marked convexity of the beak are observed in the larger specimens. This is taken to denote mature specimens. Absence of these characters is thus indicative of juveniles.

Schizodus piedmontensis, a new species, is closely related to *Schizodus shansiensis* Chao (Chao, 1927: 11–13). This affinity is of particular interest in view of Chao's observation that:

> . . . our shells are comparatively small and none of them attain the size mentioned by Meek (i.e., for *S. wheeleri*). The reduction in size, however, may be accounted for by their occurrence in a layer of highly carbonaceous shale (Tumen shale), as *all the species from the same bed are somewhat dwarfed.* (Italics mine.)

Chao's specimens had the following size range: length, 13.5 to 24.5 mm.; height, 10.5 to 19.6 mm.; thickness, 7.0 to 10.0 mm. Chao does not provide critical evidence for dwarfing other than that given in the above quotation.

It is possible that *Schizodus wheeleri* Meek is a polytypic species of which *S. shansiensis* represents a geographic race. Present data on the duration of planktonic larval stages of Mollusca in the ocean (Durham, 1951: 1522) indicates that these stages last about three weeks and are infrequently transported distances greater than 900 miles over oceanic depths. On the other hand, evidence from the distribution of Tertiary and Recent molluscs shows that identical, or closely related species, can and do occur over distances up to 3,000 miles (Vredenberg and Hertlein, cited by Durham, idem). In this respect, a glance at the latitudinal occurrence of *S. wheeleri* is of interest. The type of Swallow's *S. wheeleri*, is from the Upper Coal Measures of Caldwell County, Missouri. This area lies close to 40° N. latitude. At a latitude approximately 40°± N. other specimens of this species occur in Iowa, Illinois, Kansas, and Nebraska. Similarly, the Chinese specimens occur within this latitude (Shansi Province). Apparent diminished size of *S. shansiensis* cannot, therefore, be attributed to any noteworthy difference in latitudinal occurrence of *wheeleri* as contrasted with *shansiensis.* (See Part II.)

The sample available to Chao was so small that one cannot eliminate the possibility of larger specimens if the sample were increased. However, if we accept the prima facie evidence that *S. shansiensis* is apparently smaller than *wheeleri*, the presence of small individuals may be accounted for in various ways without appealing to dwarfism. Among others, the following may be noted: selective bottom sorting of comparable size grades; the specimens may all be immature individuals; it is to be expected that within a polytypic species range, variation in size will occur. In light of the incomplete documentation in Chao's paper, none of these alternatives can be excluded. Yet the possibility of *S. shansiensis* being a dwarfed form cannot be discarded either.

Chao's conclusions may have been in-

fluenced by the generally small size of all forms found in the Tumen beds and by the numerous references to the association of black carbonaceous shales and dwarf faunas. No adequately documented and described fauna of the latter type is known to the writer.

Reasoning as Chao did, we might compare the "Dry shale" species *S. piedmontensis* with *S. shansiensis* and observe that no specimen attains the smallest size attained by the Chinese species. This, however, does not prove dwarfism. Even though the size range for *S. piedmontensis* is considerably smaller than that described for previously mentioned species of this genus, no conclusions can be reached regarding dwarfism until a larger sample is available.

Conclusion: Both adult and juvenile specimens of *Schizodus piedmontensis* are represented in the "Dry shale fauna." The data are insufficient to establish or to refute dwarfism.

Aviculopecten sp. undet. I.—Determination of the growth stage of an *Aviculopecten* involves the following factors, among others (cf. Newell, 1942): Pectinacea costae increase in number with age (idem: 46); concentric growth lines increase in number with age (idem: 49, fig. 18); in specific instances adults may have length greater than width while immature specimens will have height greater than length (idem: 56); continuous increase or flare in the umbonal angle reaching a maximum at maturity (idem: 61, cf. *Aviculopecten halensis*, p. 59); marked curvature of anterior umbonal folds (idem: p. 87, *Streblochondria condrai*).

The most valuable of the above criteria for the specimen at hand is the apparent gentle or moderate curvature of the poorly defined umbonal folds. Taken together with the subdued beak curvature, this would seem to indicate an individual approaching maturity. Study of Newell's table of measurements of specimens in several species of *Aviculopecten* indicates that only in one species, *A. halensis*, are all specimens in the dimensional range of the single individual of the "Dry shale" species.

Newell observed (idem: 59) that "lacking sufficient material, it is not easy to prove that they are not juveniles. The flaring curvature of the anterior umbonal slope, however, suggests that the types are approaching maturity." The six external molds of the left valve of the species Newell discussed occurred in silty black and gray noncalcareous shale associated with bryozoans and *A. arkansansis*. He believed that this species was synonymous with *A. halensis* which occurs imbedded in a matrix of dark gray oolitic limestone. The only other American species of these small size dimensions is *A. phosphaticus* from the phosphate beds of the Phosphoria formation of Wyoming (maximum height = 6.2+ mm.). Here, too, Newell (idem: 55) states that it cannot be ascertained from a single specimen whether or not "the holotype is a normal representative of the species."

On the other hand, the table of measurements referred to above shows that for at least three species, juvenile stages are in the dimensional range of the "Dry shale" species. Everything considered, the writer inclines to the interpretation that the single representative of the "Dry shale" species attained a juvenile growth stage.

Conclusion: The single specimen of *Aviculopecten* sp. undet. I in the "Dry shale fauna" probably represents a late juvenile stage.

Aviculopecten sp. undet. II.—A single specimen of this species is available in the present collection. In light of the discussion of criteria above (see *Aviculopecten* sp. undet. I), it is sufficient to state that the numerous concentric grooves and abundance of costae indicate that the specimen probably attained an early mature growth stage. Whether the size attained in early adulthood is normal for this species cannot be ascertained since a new species is involved.

It should be noted that the size of this specimen is considerably smaller than that for *Aviculopecten* sp. undet. I. Whether this implies dwarfism cannot be either proved or denied.

Conclusion: The single specimen of *Aviculopecten* sp. undet. II in the "Dry shale fauna" probably represents an early adult growth stage. Although the size is extremely small, nothing conclusive can be said regarding dwarfism. The specimen may or may not be a dwarf.

Nuculanella piedmontia.—Most of the

sample falls in the range of 2.5 mm. to 4.5 mm. in length. In view of the small sample of eight specimens, graphic analysis is inconclusive. Thus, only the morphologic criterion can be used.

Traces of a few concentric growth lines (three or four) can be seen on several of the specimens. This is interpreted to denote a juvenile growth stage. The range for height is 3.0 mm. to 4.5 mm. Thus, it can be seen that the size range for both length and height is small. Hence, it appears that no significant growth increment separates the largest from the smallest specimen in the sample. It therefore seems that the entire sample is probably juvenile.

Conclusion: The specimens of *Nuculanella piedmontia* in the "Dry shale fauna" represent juvenile stages of growth.

Pleurophorus pseudoblongus.—The small sample precludes graphic analysis. Some of the smaller specimens retain traces of a very few (three or four) concentric growth lines. These specimens are probably juveniles. The size spread for height is very narrow, most specimens falling within the range of 3.0 mm. to 4.5 mm. The spread for length is greater (6.8 mm. to 10.0 mm.) but no trend is discernible.

Specimen Number	Height (mm.)	Width (mm.)	Number of Whorls
12	3.5	2.9	$2\frac{1}{4}$
15	4.3	3.4	$2\frac{3}{4}$
16	4.4	3.6	$2\frac{3}{4}$
1	4.7	3.7	$2\frac{3}{4}$
13	5.4	4.7	$2\frac{7}{8}$
10	11.7	9.7	$3\frac{1}{4}$

Specimens larger than specimen number 10 do not have the inner whorls preserved. Nevertheless, the above tabulation is sufficient to show that there is a progressive increase in the number of whorls with increasing height and width. Specimens greater than 11 mm. in height may be expected to show an increased number of whorls. These would probably correspond to late maturity. The fact that few such specimens occur in the present sample, supports the interpretation that most of the specimens represent juvenile stages.

Conclusion: The specimens of *Kansana discoidalia* in the "Dry shale fauna" represent juvenile growth stages. A few undwarfed adults are also present.

Strobeus cf. *S. paludinaeformis.*—Knight (1931: 213–215), in his study of *Strobeus paludinaeformis*, gives critical dimensions which are summarized below:

Growth Stage	Type Number	Height (mm.)	Width (mm.)	Apical Angle	Number of Whorls	Ratio H/W
				(degrees)		
A half grown individual	(E)	13.3	8.1	68	8	1.63
A three-quarter grown individual	(D)	18.0	10.3	75	9	1.61
A mature individual	(C)	16.0	15.7	69	10	1.65

Conclusion: Some of the specimens of *Pleurophorus pseudoblongus* are apparently juveniles. The growth stage of the rest of the specimens is undetermined. For the latter, nothing conclusive can be said regarding dwarfism.

Kansana discoidalia.—The twenty-four specimens of this new genus and species are inadequate for graphic analysis. A sufficient number of specimens, however, are present to provide useful morphological data relevant to growth stages.

All "Dry shale" specimens are considerably smaller than the smallest of the above types. The concave sides to the spire correspond in *S. paludinaeformis* to "neanic" stages (Knight, idem: 214) and probably have the same interpretation in the "Dry shale" species. However, in adult stages, the ratio of h/w should increase to greater than 1.86 in the "Dry shale" species whereas in *paludinaeformis*, type B, with twenty whorls it has a ratio of only 1.78. It is this difference which prevents direct assignment of the present species to *paludinaeformis*. Never-

theless, the two species are sufficiently close to allow the conclusion that the "Dry shale" species represents immature forms only.

Conclusion: The specimens of *Strobeus* cf. *paludinaeformis* of the "Dry shale fauna" represent immature individuals.

Euphemitella emrichi.—Warthin (1930: 44) observed of the microscopic *Euphemites carbonarius* that even specimens as small as 0.75 mm. in diameter were recognizable. All of the gastropod species which he described (*Euphemites* included) were composed of small individuals. This led him to conclude that (a) only young specimens were present, and (b) that even adults did not reach great size. In other words, these species had a small upper size limit. However, he did not completely eliminate dwarfing, stating that the small gastropods were "little, if at all dwarfed." As noted earlier, while several authors (Sayre, Gayle Scott) refer to "degree of dwarfism," this is a vague concept lacking necessary criteria.

Sayre (op. cit.) studied 22 genera and 47 species of gastropods in the Drum limestone of Kansas and Missouri. He compared small specimens with those of established normal size wherever possible and reached the conclusion that his gastropods were "dwarfs." The limitations of this approach have already been noted. The establishment of the growth stage, provision of tables of critical dimensions for alleged dwarfs and normal gastropods, etc. are needed.

The point Warthin raised was later reiterated by Kummel (1948), namely, that a given species might have a low upper size limit. This appears to have been the case for *Euphemitella emrichi.* Nevertheless, the species shows a size spread below this small upper limit. It is here we must look for evidence on growth stage. However low the upper size limit, the size distribution below it will represent one, some, or all growth stages.

Graphic analysis of the sample of *E. emrichi* is inconclusive since the sample is small. Nevertheless, a distinct trend is discernible in the size distribution. Specimens bulk in the range of from 2 mm. to 6.5 mm. for length and from 2.5 mm. to 4.5 mm. for height. A few specimens fall on either side of these ranges. The umbilicate character of the shells of the entire sample provides the necessary information. This character has been generally associated with immature stages. Thus, all the specimens are probably juveniles. The smaller specimens probably represent early juveniles and the larger specimens, late juveniles.

Two specimens of this new species were found weathered out of shale near each other. The question of dwarfism might be raised to explain the large size difference of the two specimens since the larger specimen is wholly calcareous, while the smaller was wholly limonitic. One might reason that the limonitic specimen is a "dwarfed" and the calcareous, a "normal" individual. However, collections from elsewhere brought together a sufficient number of specimens to show that a limonitic specimen (No. 17 of this sample) was almost as large as the calcareous specimen. It had a greater maximum apertural width and diameter but was 0.3 mm. smaller in height. The calcareous specimen fitted the size distribution characteristic of the whole sample and was umbilicate. Hence, both limonitic and calcareous specimens were found to be juveniles.

Conclusion: The specimens of *Euphemitella emrichi* of the "Dry shale fauna" represent immature growth stages.

Straparolus (Euomphalus)? gladfelteri.—When we compare size distribution in other species of this genus (Knight, 1934), a half-grown individual of *S. savagei* has 5½ whorls and a height equal to 6.25 mm. with a width of 11.0 mm. This is much larger than the largest size attained by any specimen of the new species. Two specimens of the new species retain what appears to be the full complement of whorls:

Specimen Number	Height (mm.)	Width (mm.)	Number of Whorls
4	4.1	3.3	2
1	4.5	4.1	2¼

The above tabulation suggests that half-grown individuals will have less than three whorls, three-quarter grown indviduals, more than three whorls, and possibly less than four plus, and adults more than four plus. This, in turn, leads to the interpreta-

tion that half-grown and three-quarter grown individuals are represented in the present sample. The largest specimen with a height of 7.3 mm. and a width of 6.2 mm., probably represents an early mature stage.

Specimens of the new species fall into three size groups based on increasing height and width and hence number of whorls. These groups do not appear to be separated by any hiatus. This indicates a normal distribution. The three size groups are: 3.0 mm. to 5.5 mm.; 5.5 mm. to 6.5 mm.; and greater than 6.5 mm. These relationships may be interpreted as follows: the first group represents half-grown individuals, the second group, three-quarter grown individuals, the third group, full-grown individuals.

Conclusion: Specimens of *Straparolus* (*Euomphalus*)? *gladfelteri* in the "Dry shale fauna" represent three growth stages: half-grown, three-quarter grown, and full-grown individuals. The full-grown individual is undwarfed.

Bellerophon wabaunseensis.—In the discussion of the genus *Bellerophon* (Knight, 1944: 43; cf. Knight, 1941: 52–54), only one distinguishing feature was given for mature individuals. A short distance within the aperture of such individuals, the inductura thickened to a pad. In the holotype, *Bellerophon vasulites*, this thickening is greatest one-quarter whorl back from the margin. The absence of marginal thickening of the inductura in the new species is a specific character. The failure of the inductura to show thickening to a pad back from the margin is valuable as a growth stage indicator. Since all specimens of the new species lack this feature, they may be designated as juveniles.

In addition, there is another type of evidence. *Bellerophon crassus* Meek and Worthen was established to embrace large specimens (some 57.4 mm. in length). Based on the above criterion, these specimens were apparently adults. White (1883: 57) also studied similar sized adults of this species. Ulrich's description (1897: 915–916) of *Bellerophon troosti* indicates that the shell was rarely 17.0 mm. in diameter. This was reported to be beneath "the medium size" for the genus. Shells of *Bellerophon platystoma* (Ulrich, idem: 918) were found to exceed the medium size for the genus. Elsewhere in the discussion Ulrich referred to two varieties of the latter species. These were said to be either identical in size with the types of Meek and Worthen (i.e., about 57.0 mm.) or much smaller, rarely exceeding 20 mm.

Reference to a medium size for a genus can be most confusing. For the problem considered here, however, it has some reference value. We may follow Ulrich and assume 17.0 mm. as the medium size for the genus. Then the 3.0 mm. to 6.9 mm. size spread of the "Dry shale" specimens is far below the medium size. One is thus left to conclude that the relative smallness is either a function of growth stage or of dwarfing. The second possibility seems unlikely in view of the morphologic criterion discussed above.

Conclusion: The specimens of *Bellerophon wabaunseensis* in the "Dry shale fauna" represent immature stages.

Hollinella gibbosa.—Since only a single specimen of this species is available, reliance will be placed on comparative measurements for a determination of growth stage. A tabulation of comparative dimensions for several hollinellid ostracods is given in Table 5.

Study of this table indicates that the "Dry shale" species closely fits the dimensions for mature non-productive females (narrow-frilled type). Thus it would seem that the "Dry shale" specimen is mature.

TABLE 5.—COMPARATIVE DIMENSIONS FOR HOLLINELLID SPECIES FROM DIFFERENT LOCALITIES

Number	Species	Length (mm.)	Height (mm.)	Ratio of L/H	
1	*H. gibbosa*	1.10	0.67	1.64	"Dry shale fauna"
2	*H. gibbosa**	1.18	0.63	1.87	Ft. Riley limestone
3	*H. nevensis*	1.12	0.66	1.69	
4	*H. emaciata*	1.09	0.69	1.57	

* 2, 3, and 4 from Kellett (1929: 208). 1–4, narrow-frilled types, non-productive females.

However, is this specimen dwarfed? Since the "Dry shale" species is close to the dimensions for narrow-frilled hollinellids from elsewhere and in particular close to these types from *H. gibbosa*, it appears to be "average" size for mature non-productive hollinellid females.

Conclusion: The single specimen of *Hollinella gibbosa* in the "Dry shale fauna" represents an undwarfed mature growth stage.

Hollinella dissimilis.—Although the genus *Hollinella* was set up by Coryell (1928: 378) for Oklahoma specimens, it was expanded and amended by Kellett (1929: 196–217) on the basis of Carboniferous material from Kansas. The genus was expanded to incorporate what the author termed "sexual trimorphism." Thus, distinct sexual types were recognized: (a) frilless forms and (b) frilled forms. The frilless forms were designated as the young of both sexes and mature males. The frilled forms were considered to represent mature females. The frilled forms were further subdivided into (a) non-productive females with narrow frills, and (b) productive females with wide frills more or less concave on the inner side.

Kellett (idem: 198–199) further observed that most frilless forms "are clearly young specimens because of their small size. No such small frilled forms were found, apparently showing that all the young are frilless." This was later elaborated somewhat by the same author (1933: 71) "the third form (has) only a row of granules or spines replacing frills. The young are *always* of this latter type. . . . " (Italics mine.)

The above definitions should establish *H. dissimilis* as a mature form since it has a frill. However, the new species is a small-frilled form which has not previously been reported in the literature. A study of critical dimensions will help in clarifying this point. (Table 6).

Kellett's precise redefinition of the genus now places all of Coryell's species listed in Table 6 in the young molt stage. *H. crassamarginata* "is small below the Neva, but in the Neva and above it occurs in distinctly larger size, the two sizes occurring together sometimes" Kellett observed (idem: 206). This presents three possible alternatives: (a) the narrow-frilled *H. crassamarginata* is mature despite its comparatively small size, (b) this species shows an increase in time, in ultimate size attained at maturity, (c) the narrow-frilled form is immature. The first alternative is ruled out because originally (1929) Kellett took the *small size* of the frilless forms and not the absence of frills as definitive of immaturity. However, since frilless forms were invariably small and no such frilled forms were found, the conclusion was reached that "all the young (i.e., the small) are frilless." Furthermore, the narrow-frilled type of *H. crassamarginata* is not only small but smaller than any other described specimens including the "immature" forms of Coryell. This fact, which alters the original definition and presents evidence not then available, has not been incorporated in an expanded definition of growth stage represented by frilless forms small or smaller than unfrilled forms.

The second alternative can be ruled out because Kellett (1933: 206) further observed of the small-frilled type of *H. crassamarginata*, that those in the Cottonwood are small. The Cottonwood, of course, is stratigraphi-

TABLE 6.—DIMENSIONS OF DIFFERENT TYPES OF HOLLINELLID SPECIES

Author	Species	Type	L* (mm.)	H (mm.)	T (mm.)	L/H
Coryell	*H. dentata*	spines instead of frills	0.81	0.50	0.38	1.62
	H. ovata	spines instead of frills	0.80	0.40	0.25	2.00
	H. regularis	frilless	0.80	0.45	0.39	1.77
Kellett	*H. crassamarginata*	narrow frill	0.66	0.57	—	1.15
	H. crassamarginata	wide frill	1.09	0.94	—	1.15
	H. similis	narrow frill	0.75	0.47	0.37	1.57
	H. similis	narrow frill	0.77	0.47	0.37	1.63

* L—length; H—height; T—thickness; L/H—ratio of length over height.

cally earlier in age than the Neva. Thus, no trend towards increase in ultimate size attained in maturity occurs in the younger beds.

The third alternative seems to conform best to the tabulation of critical dimensions given above for juvenile narrow-frilled forms. If we accept this alternative for small narrow-frilled forms of *H. crassamarginata*, we must do the same for the small narrow-frilled forms of *H. similis*. Accordingly, the "Dry shale" narrow-frilled type of the new species is here designated as juvenile. Following Kellett's definition, we may further classify the specimens as non-productive females.

Conclusion: The specimens of *Hollinella dissimilis* of the "Dry shale fauna" represent juvenile growth stages.

Bairdia beedei.—It is possible to compile a table of dimensions of this species from data in the literature which can serve as a frame of reference for the determination of the probable growth stage represented by the "Dry shale" specimen.

Length (mm.)	Height (mm.)	L/H
Bairdia marmorea (*beedei*) Kellett (1934: 127)		
1.01	0.58	1.74
1.06	0.58	1.82
1.07	0.59	1.81
1.10	0.60	1.85
Bairdia beedei Ulrich and Bassler, holotype (1906: 149–164)		
1.22	0.75	1.62
Bairdia beedei Ulrich and Bassler (Kellett, 1934: 124)		
1.24	0.75	1.65
1.30	0.75	1.73
1.35	0.77	1.75
1.42	0.83	1.75

Cordell (1952: 84) observed that

> the holotype of *B. beedei* from the Cottonwood shales of the Kansas Permian, is much smaller than the adult specimens from the Pennsylvanian. However, as some of Kellett's specimens of the species from the lower Permian are as large as the typical Pennsylvanian carapaces, it is believed that the holotype is either from a *depauperate faunule* or in a specimen affiliated with *B. marmorea* Kellett, which apparently consists of immature molts of *B. beedei* (Italics mine).

Reference to the above table indicates that the holotype fits into what appears to be a progressive series of molts. Thus, it most probably represents either a late immature or early adult molt. This rules out that part of Cordell's suggestion which would assign the holotype to a "depauperate faunule."

The dimensions given by Coryell and Booth for *Bairdia hurwitzi* (=*beedei*) compare closely with those for the "Dry shale" specimen:

	Length (mm.)	Height (mm.)	L/H
Wayland shale specimen	1.3	0.76	1.7
"Dry shale" specimen	1.2	0.72	1.7

By reference to the above tabulation, it seems apparent that the "Dry shale" specimen belongs to a growth stage close to that of the holotype and accordingly, is designated as late immature or early adult. The "Dry shale" specimen fits into the above series rather than, as might be expected, being an anomaly if dwarfism were operative. Dwarfism may be completely ruled out in this instance.

Conclusion: The single specimen of *Bairdia beedei* in the "Dry shale fauna" represents a late immature or an undwarfed early adult stage.

Bairdia subconvexa.—The holotype of this species was collected from the Wayland shale. A comparison of the "Dry shale" specimens with the holotype is given at the top of the next page.

It will be seen from the comparative measurements that one of the "Dry shale" specimens is very close to the holotype's growth stage. While there are not sufficient data available to tabulate the dimensions for successive molt stages, the discussions of several authors throw additional light on the sizes found in the genus *Bairdia*.

Cordell (1952: 92–94) uses such terms as "carapace of medium size" (for the genus); "average in size," "small for the genus." Nevertheless, by reference to the actual dimensions, the "Dry shale" specimens in Cordell's terms would be definitely below

	Length (mm.)	Height (mm.)	Thickness (mm.)	L/H
Wayland shale holotype	1.15	0.57	0.45	2.0
"Dry shale" specimens:				
Lower 10″	1.15	0.62	0.40	1.8
Upper 10″	1.07	0.65	0.42	1.6

"medium" size for the genus and somewhere between "small" and "average" for the genus.

There is another approach to this problem. The growth stage of any ostracod molt can be approximated if there is a large enough sample (Spjeldnaes, 1951). When single or few specimens only are available, other approaches can be employed. Kellett (1934: 123) emphasized that variation of the ratio of length to height within an ostracod species may be considerable. This would apply within the same bed and at the same locality. It should certainly temper any qualitative designations as to age based on one or a few specimens. There is a certain amount of difference between mature and immature molts of species of *Bairdia*. This difference is usually expressed in *the more pointed ends of immature molts* (Kellett, idem: 123). The posterior end of the "Dry shale" specimens is pointed with sufficient distinction to indicate a late-immature growth stage.

An additional consideration favors this interpretation. Juvenile stages appear to predominate in any considerable sample of ostracod molts (Spjeldnaes, idem). Where there is a single or a few specimens, the likelihood is that they will be juveniles.

Conclusion: The two complete molts of *Bairdia subconvexa* in the "Dry shale fauna" represent a late juvenile growth stage.

Neobeyrichiopsis emporiensis.—A curve was obtained by plotting length against frequency (figure 6). Interpreting this curve after the plots of Spjeldnaes (op. cit.), the following facts emerge: (a) at least two successive molt stages are represented by the 41 specimens of the present sample, (b) molts with a length equal to 1.0 mm. or greater, represent adults. Later juvenile stages constitute four-fifths of the sample. The adult sizes agree well with those for ostracods in general (Scott, 1948).

Conclusion: The specimens of *Neobeyrichiopsis emporiensis* of the "Dry shale fauna" predominantly represent juveniles. One-fifth of the sample represents undwarfed adults.

RESTATEMENT OF THE FINDINGS

Each of the 21 elements of the "Dry shale fauna" was studied individually. Different criteria were employed to determine growth stages. For six species, the evidence was inconclusive. These species include: *Pleurophorus? dryensis, Pleurophorus pseudoblongus, Nuculanella piedmontia, Schizodus piedmontensis, Aviculopecten* sp. undet. I and II. The evidence for fifteen species was conclusive. Only one of these species, *Imitoceras grahamense*, appears to contain true dwarfed adults. In the remaining 14 species. where adults were present, they were found to be undwarfed. Many of these species had a low upper size limit. All other specimens within these 15 species were shown to be juveniles.

PALEOECOLOGY

A comprehensive and general review of the environment of Pennsylvanian life in North America has long been available (Moore, 1929: 459–487; Weller, 1930: 129–130). It is within this general framework that the more local and specific environment of the "Dry shale fauna" is reconstructed in the present section. As an introduction to the discussion that follows, Table 7 is presented.

The figures given in Table 7 are based on the total number of usable fossils collected from a given formation. Thus, for the Dover shale partings (localities Dover P-1, P-2, P-3), the total sample included 697 limonitic fossils. The size grade analysis shown in per cent indicates that for the first column on the left 0.14 per cent of the

TABLE 7.—SIZE GRADE ANALYSIS OF THE "DRY SHALE LIMONITIC FAUNA" REGARDLESS OF SPECIES**

Size Grade (mm.)	Dover Shale Partings N=697 Per cent	Lower Dry Shale N=963 Per cent	Upper Dry Shale N=21 Per cent
32–16	0.14	0.10	—
16–8	7.03	11.20	4.80
8–4	59.60*	63.80	52.30
4–2	32.70	26.60	38.00
2–1	0.53	0.10	4.80

* A negligible number of calcareous specimens are included in these figures.
** Ostracods excluded.

total sample of 697 fossils falls in the size grade 32–16 mm. while 7.03 per cent of 697 occurs in the 16–8 mm. size grade, etc.

The table further indicates that in each of the three shale zones shown, the major grade size of limonitic fossils was 8–4 mm. More than 90% of the entire sample in each horizon falls between 8–2 mm. This suggests that the competence of bottom currents to move the larger detritus represented by limonitic internal fossil molds on the bottom muds was practically constant during the times represented by these beds.

Paleoecologic significance of known stratigraphic relationships.—The upper shale partings of the Dover occur in the interval separating a lower fusulinid and an upper algal limestone. The collecting localities in southern Kansas near Piedmont all yielded one or several species of the typical "Dry shale limonitic fauna." In the northern localities around Emporia, components of the limonitic fauna occurred directly over the upper algal (*Osagia*) limestone of the Dover in the Dry shale.

Pennsylvanian fusulinds in general (including *Triticites ventricosus*) lived offshore in a very shallow but open sea environment. The depth probably ranged from 5 to 50 feet. In this environment they pursued a benthonic existence. The size and heaviness of the test is considered to preclude a floating existence. The size is also thought to be indicative of warm as well as shallow waters since species are reported to be smaller in cold waters. The Dover fusulinids at locality Dry N, were not only abundant, but very well preserved. This factor supports the view that they thrived in a comparatively quiet environment in which wave action was slight (Galloway, 1933: 391; Moore, 1929: 467; Dunbar and Condra, 1923: 128; Thompson, 1948: 7–8). There is no evidence that the Dover limestone fusulinids did not attain normal size. Elsewhere, some species of *Triticites* have been reported to be so far below normal size as to be either immature or stunted (Dunbar and Condra, idem: *Triticites secalicus*).

The dibunophyllid coral in the Dover limestone occurs at locality Dry N (Jeffords, op. cit.: 619–621) and at Dry C-2. Algal beds occur at the Emporia localities. These occurrences suggest probable marine conditions. These conditions generally appear to have been warm, shallow, well-lighted waters in which clay or lime-mud turbidity was absent. Such turbidity is known to choke off algal growth.

Thus, prior to and after deposition of the Dover shale member, conditions were as indicated above. In addition to fusulinids, and the algal growths and corals, typical calcareous marine forms abounded.

The interval represented by deposition of shale between the two limestone members of the Dover, introduced clay-mud turbidity into the clear shallow sea. While this clay-mud accumulated on the sea bottom, debris from the underlying Dover limestone member became incorporated in it. In other words, a period of extreme shallowing of the sea apparently occurred after deposition and consolidation of the fusulinid limestone member. During that time some of the debris of weathering accumulated on the sea floor. Such detrital material occurs in minor quantities in the Dover shale interval. This suggests that only a short time elapsed before clay-mud was deposited on the marine eroded surface of the Dover. The material included coarse sand-size detrital quartz, fragments of calcareous fossils, detrital red chert. Coal fragments, as already noted may have been originally eroded from the Nyman coal horizon.

At the end of the Dover fusulinid phase, there apparently was an extreme shallowing of the sea leaving the coastal area under very low water. Most likely the presence of

electrolytes caused flocculation and deposition on the bottom of a dark gray clay-mud. The bottom mud probably was rich in organic debris and microorganisms. This conclusion is suggested by the limonitic fauna. Bottom muds and overlying waters may well have been the feeding grounds of enormous numbers of juvenile ammonoids, brachiopods, pelecypods, and gastropods, and lesser numbers of adults. In time, such conditions would result in a badly ventilated environment.

Much has been written about fouled bottom environments (Andrussow, 1897: 1–12; MacDonald, 1919: 263–268; Strøm, 1933: 356–369; Kuenen, 1950: 9–14). The environmental significance of shales in general has been considered (Krumbein, 1949: 101–108; Trask, 1951: 44; Grim, 1951: 226–231). These studies provide little specific data on the paleoecological interpretation of dark gray shales. As will be developed later, more is known about black, red, and green shales.

While there is no direct evidence that bacteria were present in the bottom muds and overlying waters of the Pennsylvanian seas, their presence seems likely. We can then postulate the presence of iron bacteria (Harder, 1919: 8–82) and sulfur-bacteria (Galliher, 1933: 52) in the overlying waters and bottom muds of Dover shale and Dry shale time. Zo Bell observed (1933: 416–425) that whether iron exists in the ferric, ferrous or metallic state in sediments, is dependent on the oxidation/reduction potential. This potential, in turn, is largely controlled by bacterial activity. If bacteria were present in the Dover shale and Dry shale seas and bottom muds, they probably exercised such controls on the particulate iron present (see Part II, for a fuller discussion of iron in sea water).

If we assume the above mechanism, then greater or lesser volumes of hydrogen sulphide would be generated. Fouling of the bottom would prevail. This explanation, of course, implies the presence of organic matter. Cases reported along the Peruvian coast and Walfisch Bay in South Africa (Brongersma-Sanders, 1948; cf. Gunter, et al, 1948: 321) indicate that mass mortality of marine animals at sea provides great quantities of protoplasm which undergoes anaerobic decay with the production of hydrogen sulphide. On the other hand, hydrogen sulphide is known to be the cause of mortality in local and special cases (Gunter, 1942: 631–633; cf. Thompson, 1952: 68). Little is known of the direct effects of H_2S on organic matter. However, in extremely low concentrations, H_2S was found to inhibit nuclear fission in *Amoeba proteus*. Mitotic velocity was decreased and the process of cell division slowed (Chalkely, 1951: 1307; Voegtlin and Chalkley, 1935: 365–383). Since copper (cf. Part II), has an equivalent effect on this protozoan and is supposed to inactivate essential enzymes, conceivably H_2S has an equivalent, though not identical, effect.

Limonite apparently is always secondary and formed at ordinary temperatures and pressures under oxidizing conditions (Palache, Berman, Frondel, 1946, I: 686; cf. Milner, 1929: 447). Its occurrence in the dark gray Dover shale most likely indicates that after formation of pyrite under environmental limitations of a negative Eh (oxidation/reduction potential), a shift to a positive Eh occurred. This allowed for the oxidation and hydration of the original iron sulphides (Krumbein and Garrels, 1952, fig. 8, p. 26) to form the oxides and hydroxides of iron. The grade size of the limonitic content of the Dover shale which is much coarser than that found in the usual shale probably has no other significance than to indicate that it was formed closer to where pyritic aggregates in the bottom muds originally were formed.

Pyritic replacements of fossils have been attributed to reactions between the sulfur of decaying albuminous matter—a protein containing about two per cent sulfur—and the iron in the enclosing sediments (Pirsson and Knopf, 1947: 74). As noted above, bacterial intervention would facilitate such decay. It would not be necessary for such shells to be deeply buried in bottom sediments or for the bottom sediments to be compacted for this replacement to occur.

The environment that followed deposition of the Dover shale member was favorable to algal-coral growth. The normal calcareous marine fauna indicates that the sea invaded the restricted environment discussed above.

Following deposition of the algal and coral

limestone phase of the Dover, the water again shallowed, leaving low water in the coastal area and again created conditions for a poorly ventilated environment. On the surface of the Dover limestone lay some calcareous debris. This indicates some amount of marine erosive action before the shallowing of the water. Thus, at the Shawnee locality, calcareous nodules occur at the base of the Dry shale immediately above a nodular algal limestone. At locality Dry E-1, fragments of Dover limestone, containing large calcareous bryozoans, brachiopods, and crinoid stems, or, these fossils weathered out, occur. Small amounts of detrital chert are also found in the Dry shale. Once again the dark gray mud was deposited on the bottom. The presence of more than 10% detrital quartz contrasts with the comparative rarity of detrital quartz in the Dover shale partings. From the viewpoint of sedimentary tectonics, this suggests that the rising elements of the source area were more active at this time. In general, the sandy and silty facies of the Dry shale may be similarly interpreted (cf. Krumbein and Sloss, 1951: 377).

Although granule and smaller size coal fragments occur in minor amounts in the Dry shale, some source for this material must be postulated. One possibility is that on a local scale in the northern area of outcrop, thin non-persistent beds of coal developed in a few small coastal swamps where peat-forming conditions came to prevail. Evidence that such conditions did prevail during upper Dry shale time may be seen in the field in the southern localities. Another possibility is that these coal fragments may be reworked material of Dover shale time. This last explanation would seem more plausible if interfingering relationships could be established for the Dry shale and the Dover shale member in the northern area of outcrop.

After some 6 feet of the Dry shale formation had been deposited, the presence of a persistent limestone stringer south of the Cottonwood River (Lyon County) bearing a normal marine fauna, indicates that the sea once again covered part of the restricted environment in the northern area. This was for a limited time only, after which the previous environment was restored.

During upper Dry shale time, in the southern area of outcrop, there is indication of a series of shallow swamps in which peat accumulated and was ultimately transformed into coal (localities Dry C-1, C-3). The coal bands are extremely thin, a few tenths of a foot thick. A relatively short period of time was involved in their formation. Between the coal and clastic limestone we get two different sequences of beds at two different localities. At Dry C-1 we get a calcareous siltstone containing the normal *Myalina*-productid marine fauna and at Dry C-3, we get an equivalent bed. However, while the bed next above the *Myalina* zone is a clastic limestone, the next bed at Dry C-3 is a dark gray argillaceous shale containing elements of the limonitic fauna found at other localities.

Thus, it is clear that immediately post-coal, in one area (Dry C-1), the sea inundated the swamp areas bringing in the normal calcareous marine fauna. This was a lime-mud depositing sea. In another area (Dry C-3) however, a shallow marine water cover extended over the swamps. Clay-mud turbidity existed in this shallow sea and flocculation was probably facilitated by humic acids. The environment thus was most likely stagnant and toxic. Instead of the normal marine fauna of Dry C-1, we find the limonitic "Dry shale fauna."

It should be emphasized that interpretation of the existence of a badly ventilated marine environment during Dover shale and lower Dry shale time is confirmed by the recurrence of nearly identical conditions (lithologic and faunal) at locality Dry C-3, representing part of the upper portion of the Dry shale. At this locality, the evidence for a restricted environment is unmistakably preserved in the rock record since we have the limonite fauna coming in above the coal.

The occurrence of red and green shales locally within the Dry shale has been reported. Most recent work (Grim, op. cit.) indicates that wherever such sediments occur within the Dry shale, there was an absence of appreciable organic material. This is of interest to our larger picture of events in Dry shale time since the very fact that such occurrences are "local" and not regional within the Dry shale lends further

support to the interpretation that, in general, a restricted environment prevailed.

Work on bottom sediments of the Red Sea indicates that hydrogen sulphide is not universally present (Strøm, op. cit.) which would allow for the existence of oxidizing conditions in local patches of the bottom. A similar situation can account for the local occurrences of oxidizing conditions in the Dry shale and accounts for the red shales. The red coloration of the shale is not due to any clay mineral component but rather to pigmentary iron oxide or hydroxide. Either ferric iron oxide or hydroxide were supplied from the source area or the existence of strong oxidizing conditions may have tended to oxidize any non-ferric iron added to the environment and to liberate ferric iron from the structures of iron-bearing silicates (Grim, op. cit.). In the Dry shale occurrences, it seems most likely that in isolated patches of the bottom, vigorous oxidizing conditions temporarily prevailed and ferrous iron in sulphides was oxidized to the ferric iron state.

The green shales which also occur locally within the Dry shale formation, probably indicate reducing conditions whereby ferric iron was changed to ferrous iron. Shales formed under reducing conditions can be green, gray, or black (Grim, idem). In his restoration of the sea bottom in Big Blue time in Kansas, Elias (1937: 413; 426–427) had the reduction of red to green silt take place in the zone of tides (littoral zone). He attributed the reducing action to organic matter. However, according to Grim (idem: 231), "a red or green argillaceous sediment means the absence of appreciable organic matter." It is quite possible, nevertheless, that even limited amounts of organic matter can facilitate reducing action. For red shales there is no doubt of the absence of any appreciable organic matter. For green shales, it is altogether possible that the mechanism outlined by Elias is the explanation of at least some occurrences. All are agreed, however, that green shales are most likely indicators of a reducing environment. Strøm (op. cit.: 365) cites the example of the soft green muds of several atoll lagunas "known to contain H_2S." Green pyritic clays of Miocene age frequently occur in deep cores from the North Atlantic (Erickson, Ewing, Heezen, 1952: 501–505). Various investigators have reported the occurrence of "soft dark green mud smelling of H_2S" in sea floor deposits along the coast of Southwest Africa from Cape Cross to south of Conception Bay and along the coast of Arabia (Brongersma-Sanders, 1948: 7–9; 94). In instances such as these, larger amounts of organic matter appear to have been present.

Paleoecologic significance of the juvenile character of the fauna.—Earlier discussion developed the point that the "Dry shale fauna" has a juvenile composition. One species in particular, *Goniloboceras goniolobum*, wherever it occurs, appears to have been composed predominantly of juveniles. Other species, such as the brachiopod *Crurithyris planoconvexa*, occur as a predominantly juvenile assemblage with a few undwarfed adults in the "Dry shale fauna." This species seems to have thrived on muddy bottoms inimical to other brachiopods (Dunbar and Condra, 1932: 346) or in black clays under acid and toxic conditions (Moore, 1929: 465). It is reported from black shales containing "depauperate" faunas. What are interpreted here as assemblages of undwarfed adults of *Crurithyris planoconvexa* are reported from several Nebraska Pennsylvanian localities. In Nebraska, at still other places, juvenile assemblages appear to have been dominant.

As a preliminary to consideration of factors that could account for the phenomenon of an entire fauna having a predominantly juvenile character, one published opinion and two possible explanations will be reviewed.

Loomis (1903: 894) observed, "On considering the small size and the simple ornamentation of the specimens [of the pyrite fauna of the Tully limestone], the first suggestion is that they are young. *But a whole fauna cannot exist of immature forms alone.* There is further uniformity in the size of the individuals of each species which can only express adult growth." (Italics mine.) This statement requires modification. An entire fauna will most usually consist of juvenile as well as adult forms. However, recent findings indicate greater numbers of juveniles are to be expected. It is also true that a whole fauna cannot continue to exist if

only immature forms prevail. However, it does not hold that intervention of selective sorting in any given area might not simulate the appearance of a whole fauna of predominantly immature forms. That is, this fortuitous intervention separates out immatures from adults and as far as the geologic record goes, it appears as if the whole fauna consists of immature forms. Obviously, this could not have been the original condition of the fauna. Uniformity of size—which is not established by the above author in terms of tables of measurements of all specimens in the collection—even though occurring among individuals of each species, does not necessarily denote adult growth. As the two examples discussed below bring out, selective sorting or sieving can account for this condition. Such uniformity of size could as readily denote juvenile growth.

In a paper on a dwarf race of lobsters on the Norfolk coast of England (Graham, 1949: 481–487), the following findings and interpretations are given. Thirty per cent of a catch of cocks and non-berried hens measured, from tip of beak to tail plate, less than 8 inches at Sheringham. This was a higher figure than for any of the other 12 stations on the English Coast where planned studies were made with the aid of cooperative fishermen. While at Sheringham eight-inch lobsters are remarkably abundant, at seven other ports ten-inch to eleven-inch lobsters occur conspicuously. The author suggests that at Sheringham the same race of lobsters as at points farther north was being fished and that Meek's theory satisfies the data best. That theory accounts for the abundance of small lobsters at Sheringham as due to their having drifted there as fry. The rarity of mature lobsters is accounted for by their having migrated upcurrent. An accompanying map showing the general current system along the coast indicates that Sheringham is situated downcurrent in the main current system. In brief, the small lobsters at Sheringham are a normal component of the lobster population, and the designation "dwarf race" a misnomer. Their predominance at Sheringham is apparently a function of the existing current system.

Fuchs (1871: 204–206) considered the general problem of the small size of the St. Cassian fauna. He noted the great number of small fry (*eine grosse Menge kleiner Brut*) and the almost voluntary exclusion of larger animals from the reef-building corals and sponges. Past students attributed the scarcity of all larger fossils to unfavorable external conditions which produced dwarfing of the fauna. However, the author observes it to be a universal rule that unfavorable external conditions lead to a reduction of the number of species, so that a species-poor fauna would be expected. It is quite the contrary with the St. Cassian fauna. Richness of forms is one of its basic characteristics. Fuchs rejected dwarfism as a solution to the problem. He later visited the harbors of Messina, where he believed he had found a key to the problem.

In the easterly shallow part of the harbor, he noted that the sea was filled with an abundance of different algae. These occur in such abundance as to proliferate an algal cover. A survey of the surface revealed swarms of little organisms which sought nurture and protection in the so-called *Algenwald*. Many of the same species of the molluscan fauna found at Steinabrunn occurred here in unbelievable quantities.

The explanation for this *eigenthumlichen Welt kleiner Bewohner* was the difference in ability to penetrate the algal cover on the part of immature (small) as contrasted with adult (large) forms. The larger forms were effectively sieved out of the area, becoming entangled in algal filaments while the small fry could readily penetrate the thick algal masses. The small molluscs attached themselves to algal leaves and stalks and continued to grow until their weight caused the algal substrate to sink to the bottom. He maintained that at St. Cassian colony-building corals and sponges similarly served as a sieve to exclude larger forms. From these observations, Fuchs concluded that the fauna of St. Cassian was not dwarfed and its uniformly small size could be adequately explained by recognizing it to be, like the living molluscan fauna of Messina harbor, the fauna of a shallow bay filled with thick algal masses.

A tiny fauna predominantly of crustaceans and fish has been reported from the modern floating sargossa meadows. With a few exceptions, minute brachiopods, etc.

have been found as associates of the graptolites (Ruedemann, 1934: 7–52). Other instances of the occurrences of minute forms in association with colony-building corals or sponges are known. An explanation similar to that of Fuchs' sieve-like separation of fry from adults is given (Kuhn, 1936: 268, item 4; Mann, 1948: 303–331).

While Fuchs' explanation is not applicable to the "Dry shale fauna," in the absence of fossil evidence of some sieve-like colonial forms (corals, algae, sponges), it might have important bearing on many of the so-called dwarf or depauperate faunas reported in black shales. This is especially so when we consider a typical explanation of the origin of black shales, which goes somewhat as follows: "Stagnation of the sea or of broad lagoonal areas by a *prolific growth of algae* which contribute their organic matter to the accumulated sediment" (Krumbein and Sloss, 1951: 377).

On the other hand, while the example of the English lobster fry is not cited as a direct parallel to the "Dry shale fauna," it has bearing on the interpretation to be given. This follows since the molluscan and brachiopod larvae are free swimming for longer or shorter periods of time, as are those of the crustaceans (Herrick, 1911: 358; Thorson, 1950: 1–45). Little is known about the larval stages of cephalopods in general and of ammonoids in particular. However, three species of living *Nautilus* had shells in the range of 25.0 mm. to 27.0 mm. (Willey, cited by Miller, 1947: 18) and these represented nepionic specimens. Miller (personal communication, 1952) favors the interpretation that since the few nepionic specimens known show a generally sandy brown coloration in contrast to early mature and older specimens which show a remarkable type of protective coloration, this may indicate a benthonic habit for nautiloid (and by inference, for ammonoid) larvae. At any rate, since adult and juvenile ammonoids often occur together in the same horizon, both very likely were vagrant benthos. It is also very probable that the fossil and Recent collections of nautiloids which contain an estimated fraction of one per cent nepionic specimens, inaccurately reflect the likely proportions of young in the original populations. This can be explained by the greater fragility of the infant shell which is considerably thinner than the mature shell and hence, more readily destroyed.

Catastrophic death of a fauna that normally lives in upper waters can be caused by a number of factors. These include rise of poisoned waters from the bottom, and influx of a salt water fauna into nearly fresh surface waters (Strøm, 1933: 361). Among other ways, bottom water faunas can meet catastrophic death by turbidity current deposition (Erickson, et al., op. cit.: 504). The cause or causes of high seasonal mortality among living marine invertebrates may be very elusive. Thus, detailed study of such likely factors of importance as metallic cations in solution, poisonous substances such as arsenic, or presence of pathogenic organisms were found to bear no relationship to the unusual mortality of English oysters during the summer of 1920 (Orton, 1923: 1–23). This contrasts with the catastrophic mass mortality of marine animals on the west coast of Florida in 1946–1947. Careful investigation (Gunter, et al., 1948: 309–323) showed that temperature, pH, salinity and oxygen content were not factors. The sole cause for the catastrophic death was attributed to the flowering of the dinoflagellate, *Gymnodinium brevis*, which, when present in large numbers, is specifically poisonous to marine animals. Exclusive of the mass death of fish, the chief invertebrates killed by this cause included barnacles, oysters, coquinas, shrimp, and the common blue crab. Similar findings are exhaustively reviewed by Brongersma-Sanders (op. cit.) who concludes "that red water (caused by noxiousness of dense populations of certain elements of the phytoplankton) and mass mortality occur especially in regions of upwelling water" (p. 63). It is interesting to note that in sediments in regions of upwelling water, there is a paucity of benthonic invertebrates (p. 97). An explanation of this kind could not apply to the benthonic assemblage of the "Dry shale."

The "Dry shale fauna" of ammonoids, pelecypods, gastropods, and brachiopods was generally of benthonic habit in early, late, or post-larval stages. Nevertheless, *the entire fauna appears to have met catastrophic death.*

Several factors have to be fitted into place in order to pursue the above explanation. First, studies of living and some fossil marine invertebrates indicate a predominance of juveniles in the samples and it is well established that the chances for survival of eggs and larval forms in the predatory and oft-times inhospitable marine environment is most precarious. Thus, the number of eggs deposited vary from a relatively few to huge quantities, thus apparently ensuring the survival of the species by invoking the laws of probability. In this manner, at least some eggs and some larval forms will pass the critical period of existence and reach full reproductive maturity (cf. Berrill, 1951: 128–132; Magalhaes, 1948: 404–405; Mattox, 1949: 352–354). Second, during larval stages which in general for many marine invertebrates are free swimming stages, a duplication of the Sheringham lobster fry example may have happened many times in the geologic past. This seems quite plausible for the "Dry shale fauna" since, as shown, the major grade size, regardless of species, is 8–4 mm. Thus, most of the specimens would have offered nearly equal resistance to current action. Accordingly, they could have drifted or been swept into the shallow coastal areas during Dover shale, lower Dry shale, and post-coal deposition in upper Dry shale time. Third, we assume for most juvenile specimens and all adults of the "Dry shale fauna" that the transfer to a benthonic habit had already been accomplished. We can then readily account for the assemblage found. We need but postulate that the shallow coastal waters and bottom sediments were excellent feeding grounds and hence attracted the different components of the fauna. Only subsequently did catastrophic death overcome all marine occupants of the fouled area. Selective bottom sorting of equivalent size grades (juveniles and adults) took place later.

Undwarfed adults in the "Dry shale fauna" can be accounted for as follows: over 90% of the entire fauna falls within the grade size range of 8 mm.–2 mm. We have here a suggestion of the bottom current competence. Any adult within this range would be moved and hence ultimately found in association with a juvenile assemblage. Recent flume tests indicate that it is the variable "effective density" which governs whether brachiopod shells will move more easily than the sand on which it rests. The competent velocity in turn is thought to be proportional to the square root of the effective density. The latter is defined as weight per unit volume when grains are immersed in water. The size and shape of the *Terebratella* shell was found to govern the initial velocity needed for movement (Menard and Boucot, 1951: 131–151). Allowing some variation due to differences in size, shape, effective density, the authors' observation can apply to the "Dry shale fauna": "unattached shells are clastic particles in the same sense as grains of sand or gravel and hence the factors governing their movement are the same." There is general agreement among hydraulic engineers that a current velocity competent to move coarse sand and pebbles is proportional to the square root of the diameter of the grains.

If one follows the interpretation that the mature imitoceratids are dwarfed, how can the presence of dwarfs in a generally juvenile association be explained? Dwarfed imitoceratids display closer suture spacing of the most adoral sutures. Mature ammonoids are recognized by this characteristic. Closer spacing of sutures during maturity probably represents normal growth superimposed on retarded growth for the "Dry shale" specimens. If so, in larval and later stages of development through early adolescence, these specimens may have been exposed to the toxic influence of ionic iron in high concentrations. Ionic iron may have indirectly contributed to retardation of growth by facilitating production of sulfoxide in the cell (See Part II). The ultimate effect on the size of the ammonoid conch as expressed at the beginning of the mature stages would be a shell of smaller than usual size. During maturity, normal growth apparently was resumed insofar as closer suture spacing of the most adoral sutures may be taken as being indicative of normal development for this growth stage. If ionic iron toxicity had been counteracted by the buffer action of organic matter, even though the water remained rich in particulate iron, conditions favorable to normal growth would have prevailed during the mature stages of the ani-

mal's life. Such reversals from retarded to normal growth are not uncommon. Numerous studies discussed in Part II indicate that when conditions having adverse physiological effects on marine invertebrates are changed in the direction of removal of the negative factor, animals tend to resume normal growth.

The dwarfed adult imitoceratids could then have migrated into a restricted area of the shallow sea where subsequently catastrophic death overcame the entire animal population. The presence of the dwarfed specimens among the pebble-necrocoenosis of the "Dry shale fauna" has already been explained in terms of the major grade size which was 8–4 mm. for all elements of the fauna.

How can we explain a repeated recurrence of the conditions outlined above, that is, in the Dover shale sea and after a lapse of time, again in the Dry shale sea in the same general area? It has already been noted that there is a statistically significant difference in the mean diameters of dwarfed adults in the older Dover shale and the dwarfed adults of the Dry shale, that of the older Dover shale being smaller. In other words, although dwarfed adults did occur among a pebble-necrocoenosis at both times, conditions affecting growth were not identical. The Dover shale dwarfed imitoceratids were apparently exposed to the toxic ionic iron environment for a longer time than the Dry shale specimens. That, in turn, could denote that the quantity of organic matter available in the Dover shale sea remained inadequate for effective buffer action for a more prolonged period than in the Dry shale sea.

SYSTEMATIC PALEONTOLOGY

CEPHALOPODA

Genus IMITOCERAS Schindewolf 1923

IMITOCERAS GRAHAMENSE (Plummer and Scott)

Plate 49, figures 22, 23, 38

Aganides ? sp. ELIAS, 1936, Internat. Geol. Cong., Rept. 16th Sess., vol. 1, p. 695.

Neoaganides grahamensis PLUMMER & SCOTT, 1937, Texas Univ. Bull. 3701, pp. 18, 350–351, 390, 502, text fig. 88 (opp. p. 402), pl. 40, fig. 4–9.

Imitoceras grahamense MILLER & OWEN, 1939, Jour. Paleontology, vol. 13, pp. 146–147, text fig. 2, pl. 20, figs. 18–20; MILLER & UNKLESBAY, 1943, idem, vol. 17, pp. 11–12; SHIMER & SHROCK, 1944, Index Fossils of North America, p. 573, pl. 234, figs. 18, 19; MILLER & DOWNS, 1950, Jour. Paleontology, vol. 24, pp. 193–194, text fig. 2, pl. 32, figs. 1–4.

Remarks.—The material at hand agrees closely with the very complete description of Miller and Downs. However, the sample available for study has provided valuable data on size distribution and measurements of distances between sutures not previously available. In addition, figured specimens show previously unfigured aspects of this species: the inner whorl, a natural section showing the cameral spacing, as well as both juvenile and adult specimens whose growth stages have been critically determined.

Measurements.—The list at the top of the next page summarizes the frequency of distribution within formations of immature and mature forms in terms of maximum diameter.

Occurrence.—Dry E-1, E-1a, E-3, E-4, E-5; Dover P-1, P-2, P-3; Dry C-3.

Figured specimens.—State Univ. Iowa, 1930, 1931, 1932.

Genus GONIOLOBOCERAS Hyatt 1900

GONIOLOBOCERAS GONIOLOBUM (Meek)

Plate 49, figures 20, 24, 25

Goniologoceras goniolobum (Meek), MILLER & DOWNS, 1950, Jour. Paleontology, vol. 24, pp. 196–200, pl. 31, fig. 9; pl. 32, figs. 5–9; text fig. 3a, p. 198 (Complete synonymy from 1877 through 1942).

Remarks.—This species has been adequately described by Elias (1938) for juveniles and by Miller and Downs (1950) for adults. The material of the present collection, composed of juveniles only, agrees well with the previously published descriptions. This sample provides valuable data on size distribution not previously available. In addition, some aspects of this species not previously figured are now provided. These show a natural section of camerae, septa, and spacing between the camerae. In addition, a high spire-type gastropod (*Soleniscus?*) occurs within the aperture of a juvenile goniologoceratid. The depth to which the tiny gastropod is imbedded and the fact that like the internal mold it also consists of iron oxide, indicates that it was

Maximum Diameter (mm.)	Immature Frequency			Mature Frequency		
	Dover Shale Partings	Lower Dry Shale	Upper Dry Shale	Dover Shale Partings	Lower Dry Shale	Upper Dry Shale
2.0	1	—	—	—	—	—
2.5	1	—	—	—	—	—
3.0	7	2	—	—	1	—
3.5	17	3	1	2	1	1
4.0	24	3	2	4	—	—
4.5	20	11	1	2	—	—
5.0	17	7	1	7	1	—
5.5	21	13	—	1	2	—
6.0	7	4	—	1	2	—
6.5	3	2	1	1	1	—
7.0	—	3	—	—	2	—
7.5	2	—	—	—	1	—
8.0	1	—	—	—	—	—

probably present pre-pyritization. This gastropod and forms of this type, most likely lived in shallow, marine waters crawling on, attached, or dug into the bottom muds. The gastropod association with an ammonoid tends to confirm the general conception of ammonoids as vagrant benthos. Since in this instance the ammonoid is a juvenile, this appears to bear out our earlier discussion that juvenile forms probably were vagrant benthos as well as the adults.

Measurements:

Maximum Diameter (mm.)	Frequency		
	Dover Shale Partings	Lower Dry Shale	Upper Dry Shale
3.0	6	3	—
3.5	5	12	2
4.0	12	14	—
4.5	14	19	1
5.0	10	19	1
5.5	9	21	—
6.0	13	17	—
6.5	12	15	—
7.0	7	18	—
7.5	2	15	—
8.0	2	6	—
8.5	2	2	—
9.0	—	6	—
9.5	1	2	—
10.0	—	4	—
10.5	2	—	1
11.0	—	1	—
11.5	—	1	—
13.5	—	1	—
15.0	—	1	—

The frequency of distribution within formations of immature forms in terms of maximum diameter is given above. Class intervals 12.0, 12.5, 13.0, 14.0, 14.5 are omitted since no specimens occur in these intervals.

Occurrence.—Dry E-1, E-1a, E-3, E-4, E-5; Dover P-1, P-2, P-3; Dry C-3.

Figured specimens.—State Univ. Iowa, 1926, 1927, 1928.

BRACHIOPODA

Genus CRURITHYRIS George 1931

CRURITHYRIS PLANOCONVEXA (Shumard)

Plate 49, figure 26

Spirifer plano-convexa SHUMARD, 1855, Missouri Geol. Survey, 2nd Ann. Rept., p. 202.

Spirifer (Martinia) planoconvexus MEEK, 1872, U. S. Geol. Surv. Nebr., Final Rept., p. 184, pl. 4.

Ambocoelia planoconvexa GIRTY, 1915, U. S. Geol. Survey Bull. 544, p. 94, pl. 11, figs. 6–7b.

Crurithyris? plano-convexus (Shumard) GEORGE, 1931, Quart. Jour. Geol. Soc., London, vol. 89, p. 43.

Ambocoelia planoconvexa (Shumard) DUNBAR & CONDRA, 1932, Nebr. Geol. Surv. Bull. 5, 2nd ser., pp. 344–348, pl. 43, figs. 12–14.

Crurithyris planoconvexa (Shumard) WILLIAMS, 1937, State Geol. Surv. Kans., Bull. 24, p. 103.

Crurithyris planoconvexa (Shumard) SHIMER & SHROCK, 1944, Index Fossils of North America, p. 329, pl. 126, figs. 18–20.

Supplementary description.—Length and breadth are rarely equal (40 specimens out of 859); breadth is infrequently greater than length (110 specimens out of 859); the predominant relationship is length greater than breadth.

Remarks.—George (1931: 43), in erecting the new genus *Crurithyris*, suggested that

"several American species that have in the past been referred to *Ambocoelia*" among which *Spirifer plano-convexus* Shumard was included "are not members of that genus and probably would be more correctly included in *Crurithyris*." Dunbar and Condra (1932: 346–347) rejected this suggestion stating that George was in error. Cooper (in Shimer and Shrock, 1944: 349) apparently accepted George's suggestion, however, for this species is placed under the genus *Crurithyris*. *C. planoconvexa*, as described by Cooper, is "small, attaining a width of 10 mm.; dorsal valve nearly flat but prominent convex umbo; outline nearly circular."

In addition to clarifying the ambiguous term used in the otherwise definitive description of this species by Dunbar and Condra, the size distribution of this species, as determined by measurements, provides information not previously available. The ambiguous term is "subequal" and occurs in the following context: "Length and breadth are subequal but the proportions vary somewhat."

Measurements.—The following list summarizes the frequency of distribution within formations in terms of width and length, with a class interval of 0.5 mm. Class interval 2.0 is omitted since no specimens occurred.

Class Interval (mm.)	Frequency					
	Dover Shale Partings		Lower Dry Shale		Upper Dry Shale	
	W	L	W	L	W	L
1.5	—	—	—	—	1	1
2.5	1	—	—	—	—	—
3.0	1	2	3	8	—	—
3.5	10	13	11	25	—	—
4.0	15	25	35	45	1	—
4.5	36	34	40	75	—	—
5.0	25	51	82	83	—	1
5.5	63	67	90	95	—	—
6.0	71	54	118	91	—	1
6.5	53	37	70	52	—	—
7.0	14	9	38	20	—	1
7.5	7	4	15	11	1	—
8.0	1	3	8	7	—	—
8.5	1	—	1	1	—	—

Occurrence.—Dry E-1, E-1a; Dover P-1, P-2, P-3; Dry C-3.

Figured specimens.—State Univ. Iowa, 1933.

PELECYPODA

Genus NUCULANA Link 1807

NUCULANA BELLISTRIATA (Stevens)

Plate 49, figure 30

Leda bellistriata GIRTY, 1903, U. S. Geol. Survey Prof. Paper 16, p 442. (Carries complete synonymy to 1900).

Leda bellistriata GRABAU, 1909, North Amer. Index Fossils, I, p. 401, fig. 512.

Leda bellistriata GIRTY, 1915, U. S. Geol. Survey Bull. 544, pp. 122–125, pl. 14, figs. 1–9a.

Leda bellistriata Stevens, SAYRE, 1930, Univ. Kansas Bull. 17, p. 106, pl. 8, figs. 7–7c.

Nuculana bellistriata (Stevens) SHIMER & SHROCK, 1944, Index Fossils of North America, p. 377, pl. 146, figs. 30–31.

Discussion.—Although Stevens originally described this species (1858: 261–262) and White (1891 :146) supplemented his description, illustrations are found in Girty (1915b: 122–125). The "Dry shale" specimens of this species fit parts of the original and Girty's supplemental and definitive description very well. Some differences in dentition are noted. There are an average of 8–9 small teeth on the short side and 15–17 on the long side, while dentition under the beak is obscure. Girty's specimens showed 10–11 (rarely 9–13) on the short side and 11–12 (rarely 13) on the long side. Beaks are situated nearer to the anterior side and, as in the specimens described by Sayre (1930: 106), the posterior extremity is slightly gaping and the shell is longer than high. This latter characteristic differs from Stevens' specimens (idem) which were described as being "as long as wide."

Measurements.—The list at the top of the next page summarizes the frequency of distribution within formations in terms of length and height with a class interval of 0.5 mm. It will be noted that no specimens occurred in the intervals 11.5, 12.0, 13.0 to 19.5, 20.5 to 24.0.

Occurrence.—Dry E-1, E-1a, E-3; Dover P-1, P-2, P-3.

Figured specimens.—State Univ. of Iowa, 1935.

Genus ANTHRACONEILOPSIS Tasch, n. gen.

Small shells gaping at both ends with beaks pointed to the shorter end, that end probably being posterior as in *Anthraconeilo;* length greater than height, truncate subelliptical in outline, greatest convexity

Class Interval (mm.)	Frequency			
	Dover Shale Partings		Lower Dry Shale	
	L	H	L	H
2.0	—	2	—	—
2.5	—	9	—	1
3.0	—	26	—	8
3.5	1	28	—	12
4.0	—	17	—	30
4.5	3	2	—	13
5.0	1	1	1	8
5.5	5	—	1	—
6.0	2	1	2	—
6.5	13	—	3	—
7.0	15	—	5	—
7.5	12	—	1	—
8.0	13	—	8	—
8.5	11	—	16	—
9.0	3	—	10	1
9.5	4	—	14	—
10.0	2	—	8	—
10.5	—	—	2	—
11.0	1	—	2	—
12.5	1	—	—	—
20.0	1	—	—	—
24.5	—	—	1	—

at umbo; dentition taxodont with 20 or more minute denticles anterior and fewer than five posteriorly; posterior and anterior scars small.

Remarks.—This genus bears closest affinities to *Anthraconeilo* Girty which was originally established to fill the gap intermediate between *Nucula* and *Nuculana* (formerly *Leda*). Like *Anthraconeilo*, it bears certain resemblances to *Yoldia* but differs in beak direction. In *Yoldia* beak direction appears to be a consistent generic character since it is always directed backward. Girty included under *Anthraconeilo* "rather large" shells which were "closed all around" and had a few large teeth on the posterior side in contrast to the many small teeth on the anterior side. In all of these respects the new genus differs from Girty's genus. *Anthraconeilopsis* consists of small shells, gaping at both ends as in *Yoldia* yet with beak directed to shorter end as in *Anthraconeilo*, and while the number of denticles on the posterior side is relatively few, the denticles are not large in contrast to those on the anterior side. These differences are deemed to be of sufficient value to merit erecting a new genus.

Genotype.—*Anthraconeilopsis kansana*, n. gen., n. sp.

ANTHRACONEILOPSIS KANSANA
Tasch, n. sp.
Plate 49, figures 4, 5

Most shells show a series of concentric grooves below the umbonal slope (five or more) which are traces of growth lines. The ventral margin is gaping in some and closed in other shells; the beaks are gently convex, not in contact; denticles at shorter end occur in a narrow flat and end at the elevated cardinal line.

Remarks.—The genus and species are based on 146 limonitic internal molds. Next to *Nuculana bellistriata* this is the most abundant pelecypod species of the "Dry shale fauna." Except for the beak being turned towards the shorter end, this species is strikingly similar to *Yoldia glabra* Beede and Rogers and this character alone will readily distinguish the two species.

Measurements.—The following list summarizes the frequency of distribution within formations in terms of length and height with a class interval of 0.5 mm. Since no specimens belonging to the intervals 11.0 to 12.5 and 13.5 occurred in this sample, these intervals are omitted from the list.

Class Interval (mm.)	Frequency					
	Dover Shale Partings		Lower Dry Shale		Upper Dry Shale	
	L	H	L	H	L	H
2.0	—	—	—	1	—	—
2.5	—	—	—	4	—	1
3.0	—	3	—	20	—	—
3.5	—	4	4	34	1	—
4.0	2	3	5	46	—	—
4.5	1	3	13	16	—	—
5.0	2	2	18	1	—	—
5.5	3	1	26	1	—	—
6.0	—	3	23	—	—	—
6.5	3	2	20	—	—	—
7.0	3	1	7	—	—	—
7.5	1	1	3	—	—	—
8.0	2	—	1	—	—	—
8.5	1	1	—	—	—	—
9.0	—	1	—	—	—	—
9.5	1	—	—	—	—	—
10.0	1	—	—	—	—	—
10.5	3	—	—	—	—	—
13.0	1	—	—	—	—	—
14.0	1	—	—	—	—	—

Occurrence.—Dry E-1, E-1a, E-3; Dover P-1, P-3; Dry C-3.

Types.—State Univ. of Iowa, 1916 (Holotype).

Genus PLEUROPHORUS King 1844
PLEUROPHORUS PSEUDOBLONGUS
Tasch, n. sp.
Plate 49, figures 33, 34

Shell small, inequilateral, elongate; ratio h/l ranges from 0.55 to 0.67; posterior margin much wider than anterior, rounded below, obliquely truncated above; anterior margin narrowly rounded below; basal margin somewhat depressed or slightly concave near the middle; beaks nearly terminal, in cardinal view convex, slightly incurved, not in contact; traces of three or four growth lines visible near basal and posterior margins of right valve.

Remarks.—This species bears closest resemblance to *Pleurophorus oblongus* Meek. It differs from the latter species in several important respects: it is usually only slightly longer than high while *oblongus* is about twice as long as high; it lacks sinuosity "at the termination of a broad, oblique impression or concavity extending from the anterior side of the beaks under the umbonal slopes to the lower margin" although it does show feeble concavity.

Measurements.—The following list indicates length, height, and thickness for specimens found at two localities:

Locality	Dimensions		
	Length (mm.)	Height (mm.)	Thickness (mm.)
Dover P-1	10.0	5.5	4.8
	7.6	4.0	3.1
	8.5	4.3	4.3
Dry E-1a	6.8	3.5	4.3
	6.7	4.4	3.5
	7.4	5.0	5.7
	6.8	4.4	3.4

Occurrence.—Dover P-1; Dry E-1a.
Types.—State University of Iowa, 1937 (Holotype).

PLEUROPHORUS? DRYENSIS
Tasch, n. sp.
Plate 49, figures 31, 32

Shell small, longitudinally oblong, somewhat less than twice as long as it is high and approximately as thick as it is high; markedly convex (bulbous) along umbonal slopes and outward to shell body except along dorsal and basal marginal areas where gently concave; this curvature has the expression, in cardinal view, of an oval tapered posteriorly and slightly indented on each side along the tapered portion of each valve; beaks slightly convex, located and turned towards anterior extremity; remnants of concentric growth lines visible on left valve.

Remarks.—This species is based on three small limonitic molds. The writer's feeling is that these probably represent a new genus as well as a new species. The distinctive feature is the curvature best seen in cardinal view. One attempt to expose the cardinal area and discover dentition was unsuccessful because of the brittle nature of the material (limonite) which readily breaks or crumbles under the slightest pressure. Accordingly, this species is tentatively assigned to *Pleurophorus* because it is closest to it in external shape and position of the beaks.

Measurements.—The following list indicates length, height, and thickness for specimens found at three localities.

Locality	Dimensions		
	Length (mm.)	Height (mm.)	Thickness (mm.)
Dover P-1	9.0	5.2	5.2
Dry E-1	6.4	3.8	3.7
Dry E-3	7.4	3.8	3.6

Occurrence.—Dover P-1; Dry E-1, E-3.
Types.—State University of Iowa, 1936 (Holotype).

Genus SCHIZODUS King 1844
SCHIZODUS PIEDMONTENSIS
Tasch n. sp.
Plate 49, figures 15, 16, 17

Shell small, subtriangular in outline; subovate posteriorly, anterior outline rounded, posterior end produced and arcuate. Valves moderately convex; greatest convexity on umbonal slope; beaks pointed, incurved, non-contiguous, occupy a position near an-

terior extremity; umbonal slope prominent forming rather distinct subround side which extends obliquely from the umbo in a direction nearly parallel to the upper posterior extremity. The ridge is characterized by a very gentle concave dorsal slope, basal margin sloping upward and meeting inward-sloping posterior margin at an angle of about 45°; dorsal margin arcuate, curving progressively downward from the beaks to obliquely truncated posterior margin. No information on musculature or cardinal teeth available from specimens at hand. In general, height greater than length. Traces of closely and regularly spaced concentric bands which extend from umbo to ventral margin.

Remarks.—The present species is quite distinct from the *Schizodus* species described and figured by Beede (1900: 155–158), Meek (1872: 203–211), White (1883: 147), Girty (1915: 130–131), Girty (1903: 439–440) and others. It bears closest affinities to *Schizodus shansiensis* Chao (1927: 11–13 and pl. 1, figs. 14–16) but differs from it primarily in that the umbonal ridge does not extend to the lower posterior extremity. This feature is shared by the Chinese species and *Schizodus wheeleri* Swallow. The new species also differs from the Chinese species in having height greater than length instead of the reverse as is the case with *Schizodus wheeleri*.

Measurements.—The following list indicates length, height, and thickness for specimens found at three different localities.

Locality	Dimensions		
	Length (mm.)	Height (mm.)	Thickness (mm.)
Dry E-1a	6.9	7.6	3.4
	3.0	3.3	2.2
	3.2	3.4	1.8
	7.3	7.0	3.7
	6.6	6.1?	2.9
	7.8	8.0	4.0
	5.4	5.3	2.9
	5.1	5.2	3.0
	3.8	4.2	2.3
Dry E-3	5.7	6.2	3.1
Dover P-1	8.0	9.0	3.5
	7.9	8.2	3.9
	7.1	7.2	3.7
	8.3	9.1	4.2
	7.4	7.4	2.7
	4.6	4.7	2.7
	4.6	5.4	2.8
	3.1	4.1	2.0

Occurrence.—Dry E-1a, E-3; Dover P-1.

Types.—State University of Iowa, 1923, 1924 (Syntype).

Genus AVICULOPECTEN M'Coy 1851
AVICULOPECTEN sp. undet. I
Plate 49, figure 21

Small *Aviculopecten* slightly longer than high; profile shows gently convex left valve and nearly flat right valve; umbonal folds poorly defined, subequal, anterior ones are slightly more prominent than posterior ones and curved forward; posterior auricles slightly longer than anterior ones. Cardinal area narrow, smooth, nearly flat; left valve shows relatively widely spaced, round, shallow costae, eight in number, obscured on shell body; no traces found on right valve which is smooth; interspaces between costae flat and unornamented except where marked by obscure fila; no cardinal or auricular costae visible.

Remarks.—Only one limonitic internal mold of this species was found in a study of over 350 pelecypods collected at random at several localities. Study of the Pectinacea as exhaustively reviewed by Newell (1942: 10–113) and of the Aviculopectens from the Upper Carboniferous, described and figured by various workers, convinced the writer that the above described specimen is a new species not properly assignable to any previously described *Aviculopecten* species. However, the inadequacy of a single internal mold for determination of such critical features as the nature of the resilifer and musculature was a sufficient deterrent to assignment of a species name.

Curiously, this species bears certain apparent similarity of ornamentation to *Euchondria subcancellata* Newell (idem, pl. 19, fig. 3a) although lack of a reticulate pattern and anterior and posterior gaping of valves, as well as the presence of umbonal folds in the described *Aviculopecten* species, eliminated its assignment to the genus *Euchondria* Meek.

Measurements.—The single specimen of this species had the following dimensions: length, 6.0; height, 5.3; thickness, 1.3 mm.

Occurrence.—Dry E-1a.

Figured specimen.—State University of Iowa, 1929.

AVICULOPECTEN sp. undet. II
Plate 49, figure 37

Small subovate *Aviculopecten*, slightly longer than high; slightly prosocline, profile shows left valve markedly convex in contrast to negligible concavity of the right valve; left valve a little larger than the right valve and in profile beak of left valve projects 0.3 mm. beyond that of the right valve; auricles subequal, badly worn; left valve shows shallow concentric grooves presumably corresponding to growth lines (seven such grooves can be seen through binocular microscope when specimen held oblique to the light); very fine costae very numerous on body of shell.

Remarks.—Only one limonitic internal mold available in present collections. Many of the critical features obscured by wear. Nevertheless, there is sufficient preservation of certain features to indicate that this is probably a heretofore undescribed *Aviculopecten* species. Pending collections which yield a larger representation of the population, specific identity cannot be further pursued.

Measurements.—The single specimen of this species had the following dimensions: length, 3.7 mm.; height, 3.0 mm.; thickness, 0.9 mm.

Occurrence.—Dover P-1.

Figured specimen.—State University of Iowa, 1940.

Genus NUCULANELLA Tasch, n. gen.

Upper part of shell triangular, convex, grading into subovate shell body; convexity maintained to pallial sinus impression below which descent to basal margin is slightly concave; shell small, height greater than length; beaks moderately convex, incurved, located close to and turned towards anterior end; hinge line marked on posterior side of beak by a line of fifteen minute denticles which end at elevated cardinal line; area containing denticles between cardinal line and beak slightly concave; anterior side of beak has five minute denticles located in an area of slight concavity.

Remarks.—The new genus bears closest resemblance to *Nuculana* Link but differs from it in three important characters: (1) *Nuculanella* is not crescent shaped and produced posteriorly, (2) beaks turned anteriorly and not posteriorly, (3) line of denticles on hinge not equal on anterior and posterior side of beaks as in *Nuculana*.

Genotype: Nuculanella piedmontia, n. gen., n. sp.

NUCULANELLA PIEDMONTIA
Tasch, n. sp.
Plate 49, figures 6, 7

In addition to the generic characters given above, some limonitic internal molds show three to four concentric depressions corresponding to growth lines that are spaced three to four mm. apart. Posterior hinge teeth appear to become smaller as they recede from the beak; anterior teeth all of the same size.

Discussion.—The pelecypod species occurring together with the new species include *Nuculana bellistriata*, *Aviculopecten*, sp. undet. II, *Pleurophorus? dryensis*, *Schizodus piedmontensis*.

Measurements.—The following list summarizes the frequency of distribution in terms of length and height with a class interval of 0.5 mm.

Class Interval (mm.)	Frequency	
	Length	Height
2.0	1	—
2.5	1	1
3.0	3	1
3.5	2	3
4.0	1	2
4.5	—	1

Occurrence.—Dry E-1a; Dover P-1, P-2, P-3.

Types.—State University of Iowa, 1917 (Holotype).

GASTROPODA
Genus STRAPAROLUS Montfort 1810
STRAPAROLUS (EUOMPHALUS)?
GLADFELTERI Tasch, n. sp.
Plate 49, figures 10, 11

Conical to discoidal shells with height greater than width. Early whorls not preserved, presumably flattened, subsequent whorls form low cone; umbilicus steep, moderately wide; outer whorls show distinct basal shoulder at culmination of a steep,

slightly concave descent, top margin of this whorl slightly rounded; some whorls show low-angled convexity directed inward from basal shoulder. In basal view the aperture culminates a short distance inward from previous whorls and right side of whorl obscures left side of umbilicus by a marginal overhang; slit, selenizone, umbilical callus lacking; no trace of ornamentation.

Remarks.—The new species is closest to *Straparolus* (*Euomphalus*) *umbilicatus* (Meek and Worthen) and to *Straparolus* (*Straparolus*) *savagei* Knight. Both of these species are closely related even though arbitrarily, as Knight explains, placed in different subgenera (Knight, 1934: 149–152). However, the width is greater than the height in both of these species, which is reversed in the new species. In addition, it differs from *savagei* in the absence of the distinctive three rounded subangular revolving ridges, and from *umbilicatus* in the lower spire. The new species is also distinct from other species of this genus and the subgenus *Euomphalus*, in having a smaller umbilicus, and in the coiling which places the aperture (seen in basal view) in a more inward position.

The species is named for Professor C. F. Gladfelter of Emporia College, Emporia, Kansas, who accompanied the writer in the field in the vicinity of Emporia and assisted in the collections of "Dry shale" fossils among which are included some of the specimens of the new species.

Measurements.—The following list summarizes the frequency of distribution in terms of height and width with a class interval of 0.5 mm.

Class Interval (mm.)	Frequency	
	Height	Width
3.0	—	4
3.5	3	2
4.0	3	1
4.5	1	2
5.0	1	—
5.5	—	—
6.0	1	1
6.5	—	—
7.0	1	—

Occurrence.—Dover P-1; Dry E-1a, E-5; Dry C-3.

Types.—State University of Iowa, 1919 (Holotype).

Genus KANSANA Tasch, n. gen.

Discoidal, very low spired, deeply umbilicate shells; height greater than width; whorls show low convexity top and bottom that converges to form fairly sharp, centered, peripheral shoulder; inner face of each succeeding whorl in plane of, and contiguous to, peripheral shoulder of previous whorl; succeeding whorls separated along entire course by narrow, shallow depression into which inner face of latter whorl makes a relatively sharp descent; shallow, very narrow, concave sinus in outer lip that appears to give rise to extremely limited dorsal selenizone which is often obscured.

Remarks.—The new genus appears to bear remote relationships to *Straparolus* as redefined by Knight (1934: 139–166; 1949: 464–465; cf. 1941: 337–338). However, the following characteristics are unmistakably distinctive: height is always greater than width; the occurrence of a selenizone; the shape of the whorls.

Genotype: Kansana discoidalia, n. gen., n.sp.

KANSANA DISCOIDALIA
Tasch, n. sp.
Plate 49, figures 1, 2

In addition to the generic characters given above, this species lacks any traces of ornamentation; the shallow depressions separating any two whorls are uniformly 0.1 mm. wide; umbilicus, steep-walled, deep, maximum shell diameter from three to four times greater than umbilical diameter.

Remarks.—Species and genus based on 24 limonitic internal molds, some sufficiently well preserved to disclose the main characteristics. Numbers of specimens are but fragments of whorls. In terms of bottom movement, the outermost whorls seemed less vulnerable to destruction than the innermost. This may be accounted for by the fact that the latter constituted a low spire elevation above the outermost whorls, and thus was subject to less support in face of hydraulic pressure and more exposed to the abrading effects of other bottom materials.

Measurements.—The following list summarizes the frequency of distribution within

formations in terms of height and width with a class interval of 0.5 mm.

Class Interval (mm.)	Frequency					
	Dover Shale Partings		Lower Dry Shale		Upper Dry Shale	
	H	W	H	W	H	W
2.5	—	—	—	1	—	—
3.0	—	—	—	2	—	—
3.5	—	—	2	2	—	—
4.0	—	—	2	1	—	—
4.5	—	—	1	4	—	—
5.0	—	—	2	—	—	—
5.5	—	1	—	1	—	—
6.0	—	—	1	4	—	—
6.5	—	—	—	2	—	—
7.0	—	—	4	—	—	1
7.5	1	—	2	1	—	—
8.5	—	—	2	1	—	—
9.0	—	—	2	—	—	—
9.5	—	—	—	1	1	—
10.0	—	—	1	—	—	—
11.0	—	—	1	—	—	—
12.0	—	—	—	1	—	—
12.5	—	—	—	1	—	—
14.5	—	—	2	—	—	—

It will be noted that no specimens occur in the class intervals 10.5, 11.5, 13.0, 13.5, 14.0.

Occurrence.—Dover P-1, Dry E-1, E-1a; Dry C-3.

Types.—State University of Iowa, 1914 (Holotype).

Genus STROBEUS Koninck 1881
STROBEUS cf. PALUDINAEFORMIS (Hall)
Plate 49, figure 3

Of small size, pear-shaped, body whorl moderately large, spire tapering with concave sides; sutures slightly impressed; siphonal folds visible but poorly preserved; siphonal channel narrow.

Remarks.—On page 376 Knight's critical dimensions for *S. paludinaeformis* were cited (1931: 213–215). The dimensions of "Dry shale" specimens tabulated below will be seen to be considerably smaller than the smallest of Knight's types. In *S. paludinaeformis*, type B with 20 whorls has a h/w ratio of 1.78. In adult stages this ratio should increase to greater than 1.86 based on the measurements given below. This and similar considerations convince the writer that although they are close to *paludinaeformis*, the "Dry shale" specimens cannot be directly assigned to that species.

Measurements.—The following list gives the critical dimensions of the three specimens of this species.

Occurrence.—Dry E-1, E-4, E-5.

Figured specimen.—State University of Iowa, 1915.

Family BELLEROPHONTIDAE

Supplementary description.—Includes forms with or without slit and slit band.

Discussion.—Description of the family (Ulrich, 1897: 852–857) includes genera in which "a slit band is always present." Despite this, Ulrich placed the genera *Warthia* Waagen, and *Mogulia* Waagen in this family even though neither had a slit or slit band. The new genus *Euphemitella* likewise lacks both of these features. It is accordingly assigned to this family as amended by the supplementary description.

Genus EUPHEMITELLA Tasch, n. gen.

This genus is erected to embrace subglobular, lirate Bellerophontidae that show variable lateral flare of the aperture, are umbilicate in the neanic stages, and lack a slit or slit band.

Remarks.—Three important discussions of the genus *Euphemites* (=*Euphemus*) in addition to the study of gastropod specimens assigned to the new genus, have led

Specimen Number	Critical Dimensions				
	Height (mm.)	Width (mm.)	Apical Angle (degrees)	Number of Whorls	Ratio H/W
3	6.7	3.6	57	6½	1.86
1	5.7	3.6	60	6	1.58
2	4.9	3.4	71	5¼	1.44

the writer to erect the new genus (Ulrich, 1897: 855; Warthin, 1930: 44; King, 1940: 150–153). The very characters specifically excluded by Ulrich and King for the genus *Euphemites* are present in the new genus. Ulrich pointed out that the umbilicus was excluded by the whorls' mode of embracing, while King stressed that no American species was umbilicate. On the other hand, Warthin assigned to *Euphemites carbonarius* (Cox), those forms which were "umbilicate in the young, more embracing in the adult." This species, *E. carbonarius*, also reported by Girty from the Wewoka, was found to be "not a valid species" by King (idem). These considerations indicated the need for a new genus to embrace the "Dry shale" forms.

Genotype: Euphemitella emrichi Tasch, n.sp.

EUPHEMITELLA EMRICHI
Tasch, n. sp.
Plate 49, figures 8, 9

Shell small, subglobular; umbilicate in immature stages; lateral expansion of aperture variable, from slight to abrupt; surface ornamented with revolving lirae 0.25 to 0.27 mm. apart.

Remarks.—This species bears resemblances to *Euphemites carbonarius* (Cox) as described and figured by Warthin (idem: 44 pl. 7, fig. 7) but not as figured by Girty (1915, p. 21, figs. 1–3b, p. 174). It is distinct from this "invalid" species by the variable lateral expansion of the aperture, nature of liration, and absence of a mesial band.

Class Interval (mm.)	Frequency					
	Dover Shale Partings		Lower Dry Shale		Upper Dry Shale	
	H	W	H	W	H	W
1.0	—	—	—	1	—	—
1.5	1	1	1	—	—	1
2.0	—	—	—	4	1	—
2.5	—	—	2	1	—	—
3.0	—	2	2	3	—	—
3.5	1	4	2	2	—	—
4.0	1	—	2	3	—	—
4.5	2	1	2	—	—	—
5.0	1	1	2	—	—	—
5.5	—	—	1	—	—	—
6.0	2	1	—	—	—	—
7.0	1	—	—	—	—	—
7.5	1	—	—	—	—	—

Measurements.—The following list summarizes the frequency of distribution within formations in terms of height and width with a class interval of 0.5 mm. With the exception of the class interval 6.5 mm., specimens occur in all the other intervals.

Occurrence.—Dry, E-1, E-1a, E-5; Dover P-1, P-3; Dry C-2, C-3.

Types.—State University of Iowa, 1918 (Holotype).

BELLEROPHON WABAUNSEENSIS
Tasch, n. sp.
Plate 49, figures 27-29

Small, subglobular, somewhat more than narrowly phaneromphalous, spiral gastropods; anterior lip with broad shallow sinus culminating in a shallow slit which gives rise to a dorsal selenizone; the selenizone slightly but distinctly raised above the surface of the shell, bordered by very shallow depressions; aperture broadly crescentic with its margins showing a generally moderate flare; this finds expression in the posterior lateral portion of the lip spreading obliquely outward and backward and partly over the umbilici; aperture continues across parietal wall forming an inductura that covers previous whorl.

Remarks.—This species differs from other described *Bellerophon* species in the variable lateral flare of the aperture; absence of inductura thickening marginally, being more narrowly phaneromphalous; and it differs from some other species by the apparent absence of stronger ornamentation.

Measurements.—The following list summarizes the frequency of distribution in terms of height and width with a class interval of 0.5 mm. No specimens occur in the interval 6.0 mm.

Class Interval (mm.)	Frequency	
	H	W
3.0	—	3
3.5	—	2
4.0	2	1
4.5	1	3
5.0	1	—
5.5	2	—
6.5	3	—

Occurrence.—Dry E-1, E-1a; Dover P-3.

Types.—State University of Iowa, 1934 (Holotype).

OSTRACODA

Genus HOLLINELLA Coryell 1928

HOLLINELLA GIBBOSA Kellett

Plate 49, figure 14

Hollinella gibbosa KELLETT, 1929, Jour. Paleontology, vol. 3, pp. 207–208, pl. 25, fig. 3b.

The single complete calcareous specimen agrees closely with *H. gibbosa*. The ridge beneath the sulcus is distinctly gibbous; the bulbous anterior node swells slightly above the dorsal margin and is set up above the general surface; the posterior node is of small diameter and somewhat inflated; convexity of valve subdued; frill of narrow type, beginning with an elevated spine approximately three-fourths of the way down on the anterior margin; the frill is incurved most sharply along antero- and central-ventral margins; a depression occurs along junction of frill and valve; anterior border shows few very short irregular spines; cardinal spine on right valve prominent.

Remarks.—The curvature of the frill in productive females is very convex, while in the narrow frilled non-productive females this is not the case (cf. Kellett, idem: pl. 25, figs. 3b, 3c). This is the only character in which the "Dry shale" specimen importantly differs from *H. gibbosa*. Since it agrees so well in most other characters, the specimen at hand is tentatively assigned to it. When more specimens are available, we shall be able to determine if the above difference is varietal or specific.

Measurements.—The single specimen of this species had the following dimensions: length, 1.10 mm.; height, 0.67 mm.; ratio of length to height, 1.64.

Discussion.—It is of interest that *H. gibbosa* is known from the Wabaunsee of Kansas (in particular the Burlingame, which is stratigraphically well below the Dry shale and the shale member of the Grandhaven). This species has not previously been found in the old Emporia limestone of which the Dry shale is a part (cf. Kellett's list of ostracods in Emporia limestone, 1935: 164.

Occurrence.—Dry E-2.

Figured specimen.—State University of Iowa, 1922.

HOLLINELLA DISSIMILIS

Tasch, n. sp.

Plate 49, figures 35, 36

Carapace subrhomboidal, length less than twice the height; anterior end gently rounded, posterior end obliquely truncate along posterodorsal margin and rounding below into ventral margin. Sulcus short and distinct but not wide, proceeds from posterior upper portion of central dorsal area in a brief course of slight obliquity towards anterior end. Anterior node bulbous, rising above dorsal margin; posterior node small, about one-half diameter of anterior node and somewhat inflated above posterior surface of valve, situated at more ventral position than anterior node. Ridge beneath sulcus gibbous; frill narrow, begins sharply near the base of the central anterior margin, continues downward and backward and thins out along the postero-dorsal margin; along ventral margin a depression marks the junction of frill and valve; scattering of granules over posterior portion of valve.

Remarks.—This species bears closest similarities to *H. gibbosa* Kellett but differs from it in the following ways: in *gibbosa* length is twice the height, sulcus is wide, cardinal spines on right valve are prominent; frill begins with elevated spine; anterior margin bordered by few short irregular spines; anterior node somewhat constricted at the base; no spines are apparently present in *dissimilis*, length is less than twice height; sulcus is narrow; there is no constriction of anterior node at the base.

Measurements	Length (mm.)	Height (mm.	Thickness (mm.)	L/H
Calcareous specimen	0.775	0.475	0.375	1.63
Limonitic specimen	0.750	0.475	0.575	1.57

Occurrence.—Dry E-2.

Types.—State University of Iowa, 1938 (Holotype), 1939 (Paratype).

Genus BAIRDIA M'Coy 1844

BAIRDIA BEEDEI Ulrich & Bassler

Plate 49, figure 12

Bairdia beedei Ulrich & Bassler, CORDELL, 1952, Jour. Paleontology, vol. 26, p. 83, pl. 18, figs. 18–20 (Gives complete synonymy from 1906 to 1935).

Carapace subrhomboidal, dorsal margin arched, broadly rounded above hingeline and gently curved on anterior and posterior

slopes; greatest ventral overlap anterocentral, distinctly depressed, anterior beak narrowly rounded with nearly straight backward swing; posterior beak with round acumination below midheight; overlap of left valve over right on all edges; dorsal contact straight; ventral contact convex except where a re-entrant sinuosity occurs anterior to the middle; greatest height slightly posterior to center; surface of valve smooth.

Remarks.—The single specimen from the "Dry shale fauna" is well preserved and complete. It corresponds very closely with *Bairdia hurwitzi* Coryell and Booth which has been placed in the synonymy of *B. beedei* (Cordell, 1952: 84). The same author indicates that he believes *B. hurwitzi* is a short form of *B. beedei*, the long form being *B. longirostris*.

Measurements.—The single specimen of this species has the following dimensions: length. 1.225 mm.; height, 0.725 mm.; ratio of length to height, 1.68.

Occurrence.—Dry E-2.

Figured specimen.—State University of Iowa, 1920.

BAIRDIA SUBCONVEXA
Coryell & Billings
Plate 49, figure 13

Bairdia subconvexa CORYELL & BILLINGS, 1932, Amer. Midland Nat., vol. 13, p. 172, pl. 17, fig. 2.

Supplementary description.—Curvature of

EXPLANATION OF PLATE 49

FIGS. *1, 2*—*Kansana discoidalia* Tasch, n. gen., n. sp. Holotype, top and apertural views, ×2, SUI 1914, loc. Dry E-1. (p. 396)

3—*Strobeus* cf. *paludinaeformis* (Hall). Apertural view, ×2, SUI 1915, loc. Dry E-1. (p. 397)

4, 5—*Anthraconeilopsis kansana* Tasch, n. gen., n. sp. Holotype, left valve, ×3, dorsal view, ×3½, SUI 1916, loc. Dry E-1. (p. 392)

6, 7—*Nuculanella piedmontia* Tasch, n. gen., n. sp. *6*, Holotype, left valve, ×4; *7*, Holotype, dorsal view, ×4, SUI 1917, loc. Dover P-1. (p. 395)

8, 9—*Euphemitella emrichi* Tasch, n. gen., n. sp. Holotype, side and apertural views, ×3, SUI 1918, loc. Dover P-3. (p. 398)

10, 11—*Straparolus* (*Euomphalus*)? *gladfelteri* Tasch, n. sp. Holotype, top and apertural views, ×3¾, SUI 1919, loc. Dover P-1. (p. 395)

12—*Bairdia beedei* Ulrich and Bassler, Right side view, ×10, SUI 1920, loc. Dry E-2. (p. 399)

13—*Bairdia subconvexa* Coryell and Billings. Hypotype, right side view, ×10, SUI 1921, loc. Dry E-2. (p. 400)

14—*Hollinella gibbosa* Kellett. Right side view, ×10, SUI 1922, loc. Dry E-2. (p. 399)

15, 16, 17—*Schizodus piedmontensis* Tasch, n. sp. *15*, Syntype, left valve, ×3, SUI 1923, loc. Dover P-1; *16, 17*, Syntype, *16*, dorsal view, ×2; *17*, cardinal view, ×2, SUI 1924, loc. Dry E-1. (p. 393)

18, 19—*Neobeyrichiopsis emporiensis* Tasch, n. gen., n. sp. Holotype, right side and dorsal views, ×10, SUI 1925, loc. Dry E-2. (p. 401)

20, 24, 25—*Goniloboceras goniolobum* (Meek). *20*, juvenile, showing characteristic sutures, ×3, SUI 1926, loc. Dry E-1a; *24*, juvenile, natural section, showing traces of 12 septa and spacing between succeeding septal walls, ×4, SUI 1927, Dover P-1; *25*, juvenile, showing high-spire type gastropod imbedded inside the aperture, ×4½, SUI 1928, loc. Dry E-1. (p. 389)

21—*Aviculopecten* sp. undet. I, Right valve, ×3, SUI 1929, loc. Dry E-1a. (p. 394)

22, 23, 38—*Imitoceras grahamense* (Plummer and Scott), *22*, natural section showing cameral spacing, ×5, SUI 1930, loc. Dry E-1; *23*, inner whorl in contact with weathered remnant of outer whorl. Note sutures. ×8, SUI 1931, loc. Dry E-1; *38*, dwarfed adult, 21 external sutures visible, note sutures crowded adorally, ×7, SUI 1932, loc. Dover P-1. (p. 389)

26—*Crurithyris planoconvexa* (Shumard). Ventral view, ×4½, SUI 1933, loc. Dry E-1. (p. 390)

27, 28, 29—*Bellerophon wabaunseensis* Tasch, n. sp. Holotype, apertural, side and dorsal views, ×3, SUI 1934, loc. Dover P-3. (p. 398)

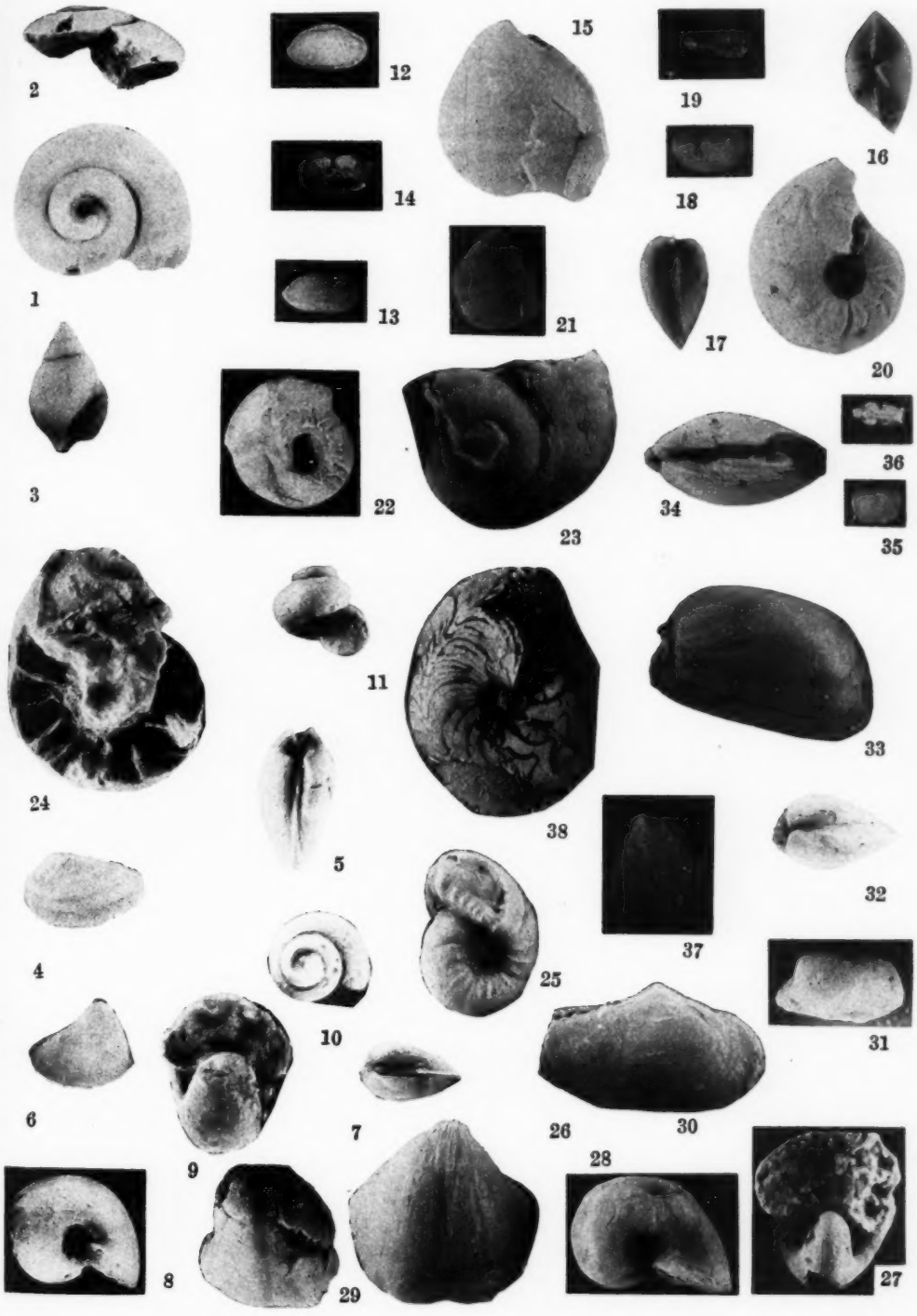
30—*Nuculana bellistriata* (Stevens). Broken right valve, ×4, SUI 1935, loc. Dry E-1. (p. 391)

31, 32—*Pleurophorus*? *dryensis* Tasch, n. sp. Holotype, left valve and dorsal view, ×2, SUI 1936, loc. Dry E-1. (p. 393)

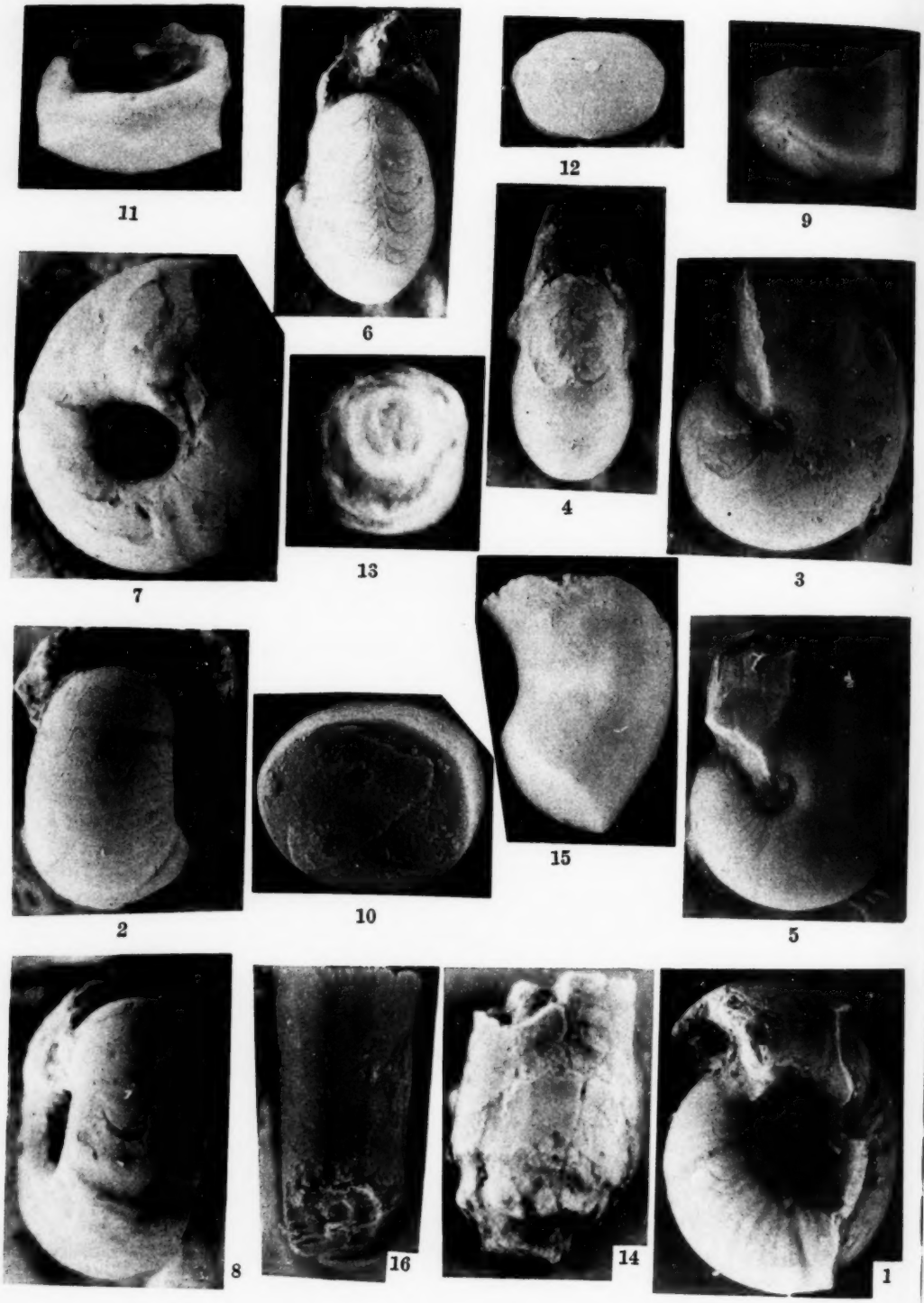
33, 34—*Pleurophorus pseudoblongus* Tasch, n. sp. *33*, Holotype, left valve, ×4; *34*, Holotype, dorsal view, ×3½, SUI 1937, loc. Dry E-1. (p. 393)

35, 36—*Hollinella dissimilis* Tasch, n. sp., *35*, Holotype, right side view, ×10, SUI 1938; *36*, Paratype, dorsal view, ×11, SUI 1939, loc. Dry E-2. (p. 399)

37—*Aviculopecten* sp. undet. II, Left valve, ×5, SUI 1940, loc. Dover P-1. (p. 395)



Tasch, Upper Pennsylvanian Dry shale fauna



Tasch, Dry shale cephalopods from Kansas

posterodorsal margin oblique and gently concave, giving slight upturn to posterior beak; left valve overlaps dorsal margin prominently only along anterior third; overlap may occur along entire free margin except the anterior edge, or may not be present along the free margin.

Remarks.—The most distinctive character of this species is the prominent overlap of the anterodorsal margin. It will be recalled that for *Bairdia* species in general, character of the dorsal overlap is deemed to be one of the "most helpful" morphologic criteria of specific value (Kellett, 1934: 123).

Locality	Critical Dimensions			
	Length (mm.)	Height (mm.)	Thickness (mm.)	Length/Height
Dry E-2				
Lower 10″	1.15	0.62	0.40	1.8
Upper 10″	1.07	0.65	0.42	1.6

Occurrence.—Dry E-2.

Figured specimen.—State University of Iowa, 1921 (Hypotype).

Genus NEOBEYRICHIOPSIS Tasch, n. gen.

Carapace subrhomboidal, minutely inequivalved, right valve apparently larger but no distinct overlap of left valve; in ventral view, right valve stands slightly higher than left; moderately deep sulcus marks carapace, begins anteriorly in central dorsal area and extends about half the width along course of slight obliquity in posterior direction, sets off more tumid posterior portion from smaller anterior lobe; both lobes merge gently in ventral swelling; hingeline faintly concave, distinctly channeled along posterior portion.

Remarks.—As originally defined (Jones and Kirkby, 1886: 434), the genus *Beyrichiopsis* was characterized by "two or more thin, curved or sinuous outstanding ribs (that) pass along the valves" ("ribs" ="crests" cf. Kesling, 1951, fig. 3, p. 100) and by a "broad fimbriate or spinous fringe (that) extends along and a little outside of the free margin of each valve." The new genus bears closest affinities to *Beyrichiopsis* but lacks both crests and fimbriate or spinous fringe. The author followed later workers in designating the greatest thickness as falling within the posterior portion (Coryell and Johnson, 1939: 214).

Genotype: Neobeyrichiopsis emporiensis, n. gen., n. sp.

NEOBEYRICHIOPSIS EMPORIENSIS
Tasch, n. sp.
Plate 49, figures 18, 19

In addition to the description necessarily given for the genus, the dorsal periphery of the posterior lobe rises slightly above the hinge-line while the much smaller anterior lobe rises from a gentle convexity that starts at the dorsal margin.

EXPLANATION OF PLATE 50

FIGS. *1, 2*—*Eoasianites* sp. undet. 2. *1*, Lateral view, ×9; *2*, Ventral view, ×9.5 (S.U.I. 1946). Loc. Dover P-1. (p. 449)

3, 4—*Imitoceras grahamense* (Plummer and Scott) Lateral and ventral views, ×8, (S.U.I. 1945a). Loc. Dry E-1. (p. 447)

5, 6—*Imitoceras grahamense* (Plummer and Scott)? *5*, Lateral view, ×13; *6*, Side view, ×14 to be compared with figures *3* and *4*, (S.U.I. 1945b), Loc. Dry E-1a. (p. 447)

7, 8—*Eoasianites* sp. undet. 1. *7*, Lateral view, ×5; *8*, Ventral view, ×4.5, (S.U.I.). Loc. Dover P-1. (p. 448)

9, 10—*Metacoceras* sp. undet. 2. Two views of fragment showing shape of suture, position of siphuncle and cross section. *9*, ×11; *10*, ×14, (S.U.I. 1942). Loc. Dover P-1. (p. 446)

11, 12, 15—*Metacoceras* sp. undet. 1. *11*, Side view showing shape of suture, ×9; *12*, End view showing position of siphuncle and cross section, ×7.5; *15*, Side view showing general curvature of conch; highlight on ventrolateral surface indicates position of nodes, ×7.5 (S.U.I. 1941). Loc. Dry E-1, E-1a. (p. 446)

13, 14—*Pseudorthoceras* sp. Two views of fragment. *13*, End view; note position of siphuncle, ×12; *14*, ×12 (S.U.I. 1944). Loc. Dover P-3. (p. 446)

16—*Mooreoceras* sp. Darkened area parallel to length indicates a slight depression, ×8. (S.U.I. 1943). Loc. Dover P-3. (p. 446)

Measurements.—The smallest specimen has a length of 0.575 mm. and a height of 0.300 mm.; the largest, a length of 1.224 mm. and a height of 0.750 mm. Arranged in order of increasing length with a class interval of 0.1 mm., the following table shows the size distribution.

Occurrence.—Dry E-2.

Types.—State University of Iowa, 1925 (Holotype).

Length (mm.)	Frequency
0.5	1
0.6	3
0.7	6
0.8	13
0.9	10
1.0	3
1.1	4
1.2	1

Part II—Theoretical Aspects of the Problem of Dwarf Fossil Marine Invertebrates

Throughout much of the geologic column assemblages of small fossils are found. As many as 50 or more species may be represented. Characteristic of such assemblages is the extremely small upper size limit of all specimens of the fauna. The composition of the fossils is usually pyritic or limonitic. However, it may be calcareous, siliceous, dolomitic or cherty. These faunas have been variously called "dwarf," "depauperate," "diminutive."

As an approach to the general problem, we can establish what may be called a "paleoecologic fence." In other words, there is a set of limiting conditions which any explanation for such faunas or any particular "dwarf" fauna must satisfy. Within this fence there are two persistent conditions: (1) almost every one of these faunas, exclusive of microfossils consists of individuals that fall predominantly into pebble or granule size grades, (2) different species and different elements of the fauna (gastropods, pelecypods, ammonoids, etc.) occur together.

The evidence of the present investigation suggests that the conditions imposed by the paleoecologic fence can best be met by the following generalization: *The end results of biological processes cannot lead to relative uniformity in size within a mixed population. The end results of sedimentary processes (sorting sieving) must be relative uniformity in size for any given sample.*

Part II of this investigation is a critique of the literature. In addition, a synthesis and application is made of the biological evidence concerning factors affecting growth, particularly retardation of growth. Part I is a detailed study of a "type" limonitic fauna—the fauna of the Pennsylvanian "Dry shale" of Kansas.

Terminology.—There are at least six terms in English and three in German which have currency. These are: depauperate (L. *depauperatus*), dwarf (A.S. *dweorh,*) diminutive (L. *de+minus*), pigmy (Gr. *pygmaios*), midget (A.S. *mycge*), runt (Scot. *runt*); *Krüppenformen* (dwarf), *Zwergformen* (diminutive), *verkümmerte Fauna* (stunted). The dictionary definitions of the most commonly used of these words show them to be synonyms or refinements of one another.

Ladd (1925: 89) tried to restrict the usage as follows: "A depauperate fauna is one in which the great bulk of the species is composed of individuals which are distinctly (but not abnormally) small, yet abundant and diversified. Such a definition excludes (1) the normal fauna which contains a fair proportion of large or medium-sized species, and (2) the dwarf fauna which is composed entirely of dwarfs of normally large individuals." As illustrative of a dwarf fauna, he named the Tully pyrite fauna described by Loomis (1903).

Despite Ladd's restrictive definition of "depauperate," it appears that he actually employed the term to denote not merely uniform small size of an entire fauna but the idea of comparable size difference as well. He observed that, "the basal Maquoketa fauna as known at present is composed of fifty-two species which rarely exceed a quarter-of-an-inch in diameter. This surely is unusual and suggests dwarfing but *as far as we know* these species are not dwarfs but make a group of animals none of which ever grew any larger" (idem: 85–86). Elsewhere in the present paper, the Maquoketa fauna

will be discussed in greater detail. It will suffice here to indicate that the above quotation requires modification in the light of Ladd's own descriptions of the fauna. In his description of *Cycloceras* cf. *clorus baffinense* (Schuchert), for example, he wrote that the Maquoketa species "resembles *Cycloceras perroti* (Clarke) somewhat. This form (*perroti*) is described from the lower Maquoketa at Granger, Minnesota but (*C.* cf. *clorus baffinense*) is *much smaller* than this form . . . " (1925: 195) (Italics mine). What Warthin (1930) and Kummel (1948) have referred to as the upper-size limit for a given species, was expressed by Ladd as "a group of animals none of which ever grew any larger." If it could be shown that for all elements of the Maquoketa fauna, or at least for all elements called "depauperate" by Ladd, the maximum sizes attained corresponded to the maximum size for the respective species, then it would be clear that the fauna is normal and not depauperate. The fact that the major grade size for all elements of the Maquoketa fauna (6.3 mm.) falls in the 8.0–4.0 mm. range, indicates that we are dealing primarily with a problem in sedimentation and not one in paleontology. This holds insofar as we have to account for the uniform small size of a diverse assemblage.

In an earlier paper on the Maquoketa (1924: 56), Ladd wrote that "the fauna at Bellevue (Iowa) . . . is a *depauperized depauperate* fauna when compared to forms at Dubuque (Iowa.)" After a description of *Ctenodonta fecunda* Hall a notation was made that "following a general rule the specimens from Dubuque are *larger* than those from southern localities (e.g., Bellevue)." (Italics mine.) It is thus evident that within the so-called depauperate fauna, a variation is implied in the maximum sizes attained. From the standpoint of clarifying terminology and bringing some degree of organization into the treatment of so-called "dwarf" or "depauperate" faunas, it appears that any conclusion regarding a fauna which is reached without the determination of its growth stages is inconclusive and confusing.

All the terms in use are qualitative statements expressive of quantitative relationships which have not been rigidly defined for paleontological purposes. We read that faunas or elements of a fauna are "slightly dwarfed," or are "depauperized depauperate." The result has been that one author's "diminutive" fauna is thought to be different from the "depauperate" or "dwarf" fauna of another. The point is that even if such differences do exist, the synonymity of different terms precludes recognition of such differences. Furthermore, many of these terms carry still other overtones of meaning. These include the causes leading to the existing conditions: starvation, crippling, weakness, none of which may have been a contributory cause in any given instance.

It is therefore proposed to drop the current usage of the term "depauperate," "diminutive," "stunted," etc., since a term expressing the upper size limit of all elements in a fauna is meaningless for paleontological purposes. It is also unsound biologically. Instead, a term such as "pebble-necrocoenosis," which denotes the major grade size characteristic of all elements in a fauna, can be substituted. Such a term might very well be utilized in sedimentation where it can be indicative of current sorting and bottom conditions. For the purposes of invertebrate paleontology, only one term seems necessary, the term "dwarf." As defined here, only those elements of a fauna should be called "dwarfs" which can be shown to be adults with an upper size limit within the juvenile size range of a given species (See figure 1).

Classification and evaluation of published information on dwarf fossil invertebrates.— References, data or discussion related to the problem of dwarfism found in the geological literature may be divided into two large classes. Class I contains statements based upon secondary sources and/or casual observation. Some statements included in this class may be based on primary sources but are inadequately documented. Class II contains more extensive statements based upon primary sources and original data and/or serious study. Statements in this class are infrequently documented adequately.

The matter of documentation is of first-rate importance in considering both classes. Adequate documentation includes provision of that kind and quantity of information and data that will permit contemporary or

future investigators to re-trace the steps of the investigator in the field and/or to re-evaluate the raw data upon which conclusions were based. Inclusion of unambiguous statements of criteria used for determining whether a given specimen is juvenile, adult, or of undeterminable growth stage, provision of tables of measurements, and similar basic data for *each* component of the fauna, are essential. The need for paleoecological data has already been stressed in connection with the problem of dwarfism (Cloud, 1948) but the documentation referred to above is even more fundamental. It is the *a priori* without which paleoecological data, even if given, are of small value.

Statements belonging to Class I, by the very nature of the context in which they are given, will generally be unaccompanied by documentation. In generalized discussions of black shales, associated "dwarf" or "depauperate" faunas are frequently mentioned (Twenhofel, 1915; Moore, 1929; Pettijohn, 1949; Krumbein and Sloss, 1951; Trask, 1951). These mentions merely require that we refer back to the original reference. If the original reference reports the occurrence of a "depauperate" or "dwarf" fauna without documentation, then we may take it that this is a "reported" but not an "established" example.

Statements based on first-hand observation, which provide information valuable in other respects, may still be inconclusive as pertains to dwarfism. Twenhofel (1915: 271–280), in his important observations on Esthonian black shales "in the making," noted the occurrence of small shells. These were reported to be "little more than a fifth or a fourth so large as the norm." At one of the Baltic localities four species were observed, none of which exceeded one-half inch in length. Adult elements of these faunas might very well be true dwarfs, but unaccompanied by data on growth stages, no conclusions can be definitely stated.

There are references by later authors (Dacqué, 1915: 424) to earlier published statements such as, "fossil faunas (corals) of Arctic seas all show dwarfing effect of unfavorable conditions when compared to the contemporary faunas in seas to the south" and "Cretaceous marine beds in Greenland have a stunted fauna which has no tropical or sub-tropical character." Thus, crinoids are reported to be small and scarce, and Mollusca small and simple (Gregory, 1906–07: 411–415). However, Holtedahl (1924: 160–165), in writing about the scientific results of the Norwegian expedition to Novaya Zemlya, commented on Gregory's statement that "since this was written much material has been gathered which does not fall in with such a view." When Holtedahl reviewed the Paleozoic faunas at different latitudes, he observed the frequent occurrence of huge Producti and Spirifers in the Middle Carboniferous of the northern latitudes. He concluded that the climate was warm-to-temperate in the present Arctic regions during Paleozoic time. Neither Dacqué, Gregory, nor Holtedahl make reference to documentation and hence, this whole debate is of the nature of "reported" rather than "established" dwarfism.

"Dwarf" faunas have been reported from specific formations. Statements of this type are quite common. In reference to the Graneros shale, for example, the following statement occurs: "1,330 feet Bentonite, light blue-gray shale, dwarf *Globigerina*" (Baker, 1951: 60). According to the staff paleontologist of the South Dakota State Geological Survey, "dwarf *Globigerina* and *Gumbelina* are fairly common with bentonite. These are apparently mature forms; they have all the chambers of the adult. This size, however, is unusually small" (Edward Bolin in Rothrock, personal communication, 1951).

A plausible explanation for the occurrence might be that volcanic ash, in reaching the sea floor, would cover and incorporate already sorted Foraminifera. Or, in a thin veneer of bentonite on the sea floor, the Foraminifera were sorted by size. In either case, it seems improbable that bentonite acted as a dwarfing agent. A recently described freshwater molluscan fauna from the Upper Cretaceous of Wyoming (Teng Chien Yen, 1952: 344–359) occurs in a porcellanite with a ground mass predominantly of fine siliceous volcanic ash. The siliceous material from the ash replaced the calcareous matter of the molluscan remains. Although many

small and some recognizably immature forms occur in this fauna, there is no evidence of a dwarfing effect. On the other hand, it is suggested that the volcanic ash may have affected the chemical environment in which these snails lived. The sinistral species are reported not to occur in contemporaneous beds nearby nor in beds above or below the porcellanite. Thus, the author postulated that this peculiar localization of sinistral coiling may be due to mutations influenced by the abnormal conditions (composition of water or soil) arising from contemporaneous vulcanism. This interpretation seems doubtful based on the lithologic evidence given. Siliceous replacement of the calcareous shells appears to indicate that all growth and morphologic peculiarities of these molluscan species had already been accomplished *prior to* the chemical release of silica in the volcanic ash.

Published information on "dwarf" Foraminifera may include numerical data. Thus *Plectogyra*, the average size of which in the St. Joe limestone in northeast Oklahoma is 0.3 mm., averages 0.9 mm. in adjacent formations. *Endothyra*, in the St. Louis limestone at East St. Louis, Illinois, are giant forms with an average diameter of 1.5 mm. while rare dwarfs have an average diameter of 0.3 mm. "Apparently dwarfed" unnamed Foraminifera occur in the subsurface Wilcox and basal Claiborne of Eocene age in Texas (E. J. Zeller and J. B. Garrett respectively, in Lalicker, 1948: 55). Statements on living Foraminifera of a comparable nature by Murray and Irvine, Mann, Cushman, Moore, et al. will be considered in the section dealing with biological evidence on factors affecting growth.

If ultimately supplemented by documentation, information of the above kind can further contribute to clarification of the general problem of dwarfism.

It has been noted of the Cretaceous of Texas that "with the exception of the Kiamitia, all the marl members (Duck Creek, Denton, Pawpaw, Grayson) of the column exhibit an abundance of small dwarfed fossils" (Scott, 1924: 7). Adkins' monograph on this fauna (1918) provides extremely useful stratigraphic and faunal information on the pyritic and limonitic fauna. No documentation is provided, however, for the dwarfism to which Gayle Scott refers. Thus, even this well-known example must be categorized as a "reported" and not an "established" occurrence of dwarfed invertebrates.

An example referred to by Shimer (1908) as one of the "dwarf faunas" is the Guelph fauna of New York State (Clarke and Ruedemann, 1903). The authors refer to a characteristic dwarfed coral, *Enterolasma* cf. *caliculus* Hall (idem: 24, and pl. 1, fig. 1), which is figured at natural size. *Dalmanella* cf. *hybrida* Sowerby (idem: 42, and pl. 4, figs. 7–8) is referred to as consisting of "a single depauperated valve." The authors observe that such genera as *Poterioceras* are characterized by species of "small size and slight development" and "appear to us as a group of dwarfed forms compared in their entirety to the small specimens with constricted apertures among late (i.e., Mesozoic) cephalopods considered as dwarfs by Pompeckj." For the entire Guelph fauna figured and described by these authors, only the three examples cited give information pertaining to dwarfism. This documentation is inadequate and when we turn to the Pompeckj (1901) reference, documentation of the type defined above is also wanting.

Bradley (1921: 515–524), in a study of the brachiopods of the Maquoketa of Iowa, reports that "a general characteristic of the new species of *Rafinesquina* and *Strophomena* . . . is that they are considerably smaller than species from other localities in the Richmond." He concludes that this is an instance of dwarfism and attributes the cause to "an ingress of mud" since "fine grains taken into the tender soft parts of these brachiopods might easily have caused an irritation that would result in the prevention of normal growth" (idem: 516). The brachiopods he studied occur in a fine-grained Maquoketa shale. Documentation of the type necessary to establish dwarfism is not provided. As for the ecology of these brachiopod genera, "*Strophomena* and *Rafinesquina* seem to have preferred bottoms receiving small quantities of mud" (Twenhofel and Shrock, 1935: 297). The explanation Bradley gives seems hardly plausible in light of this.

In a survey of Pennsylvanian invertebrate faunas of southeastern Kansas,

Williams (1937: 103) makes the following observation: "The limestone six feet above the Bevier (coal) is not very fossiliferous and except for *Serpulopsis*, our collection from it has only some brachiopods, most of which are of *Crurithyris planoconvexa* (Shumard). The prevalence of small individuals in the collection suggests a depauperate fauna." This is most likely a small pebble-necrocoenosis rather than a "depauperate fauna." The same paper (idem: 93) states that "small gastropods, occasional small cephalopods, and small pelecypods are the predominating fossils in some calcareous zones that are also pyritic or otherwise ferruginous. These suggest that depauperizing conditions existed when these beds were deposited."

The probable influence which iron may have as a dwarfing agent will be considered in a later section. However, in passing, it might be observed that mere simultaneity of occurrence of two conditions by themselves has no determinative value as to dwarfism. The two conditions might be general smallness of components of a fauna and the presence of pyritic or limonitic sediments. On the other hand, the small fauna may be pyritic or limonitic.

References to so-called dwarfism among faunas found in the Tumen shale of China (Chao, 1927), the Drum limestone of Kansas and Missouri (Sayre, 1930), the Cottonwood shales of the Kansas Permian (Cordell, 1952), are discussed in Part I. Here it may be noted, however, that none of these studies either contain or make reference to documentation. Several dwarf varieties of mollusks are reported in various New Mexico localities (Shimer and Blodgett, 1908: 53–67) and as far north as Colorado. These include *Lima utahensis* Stanton, the size reported being one-half that attained at the type locality. *Ostrea anomioides* var. *nanus* Johnson reported to be a dwarf form of the parent species, and *Ostrea lugubris* Conrad. Stanton (1893: 55–71) distinguishes three varieties of *Ostrea lugubris* Conrad in the Colorado formation. He states that Conrad's type represents "a variety that was dwarfed by unfavorable conditions while the same species under more favorable circumstances reach the large size of *O. bellaplicata* and *blacki*." For the purposes of establishing whether these mollusks are true dwarfs, the nature of the documentation in both of these papers is most inadequate. Growth stages do not appear to be considered while emphasis is placed on comparing the size of the fossil at hand with the holotype. It appears that the modern concept of species as populations showing marked differences in maximum size attained (Mayr, 1949: 102-122) would require discarding determinations of dwarfism based on the older approach of "checking against the holotype."

Croneis and Grubbs (1939: 598–612) report on a fauna found in Silurian sea balls and state that a more detailed description of the fauna would be released shortly by the junior author (Grubbs). However, the *Bibliography of North American Geology*, 1939–1949 lists no paper on this subject. This is mentioned here because the general survey of the fauna led the authors to reject the supposition that the fauna was composed mainly of young individuals. Dwarfism was the preferred explanation. Since the present review of the literature is undertaken to clarify the nature of the evidence upon which statements regarding dwarfism have been based in the past, it is more important to know that documentation is lacking for this fauna than to have the findings. The findings are, nonetheless, of much interest. The long dimension of all fossils ranged from less than 1.0 mm. to more than 20.0 mm., with an average of less than 8.0 mm. The authors apparently paid some attention to growth stages although whether these were critically established is not known. Thus, mature brachiopods, crinoids, pelecypods of species which ordinarily attained larger dimensions were reported. In addition, undwarfed bryozoans that dominated the fauna and a normal and larger than normal ostracod, *Beyrichia* (greater than 3.0 mm. in length) was also found in this fauna. The authors write that "if dwarfing has occurred, the environmental agencies which produced the dwarfed conditions were either not operative or not uniformly effective for all the invertebrate groups." Like Bradley (op. cit.), the authors follow de Lapparent (1906: 132–133) and postulate that "the introduction of mud and silt into a normally clear sea, if extended over several seasons, could conceivably disturb the eco-

logical equilibrium of the marine organisms and result in a dwarfed fauna" (idem: 611).

The major grade size of the above fauna was apparently 8.0 mm., hence, a pebble-necrocoenosis. What probably happened was that bottom sorting activity first segregated fossils of comparable sizes as indicated by the fact that they occur in nodules, which in turn, were formed by the rolling action on the shallow sea floor. After segregation, the postulated turbulent wave action rolled lime mud and argillaceous material into balls held together by incorporated bryozoans. These balls gradually rolled over the area in which the pebble necrocoenosis was distributed and incorporated them along with new increments of mud. No definite conclusions can be reached as to whether this fauna consists of dwarfed elements or not. The limited evidence available would seem to indicate that sorting and not dwarfing was involved.

An interesting example of reference to and brief discussion of a dwarf fauna is the abstract on "Dwarfed Gastropods in the Basal Guttenberg, S. W. Wisconsin" (Ball, 1935: 384). "Several species of diminutive gastropods characterize the fauna and are generally phosphatic. . . . Higher in the bed are non-phosphatic fossils which include corals, echinoderm fragments, and brachiopods of normal size." This abstract is cited in the European literature in support of one author's discussion of "dwarf gastropods" (Boni, 1942). Yet, the "studies in progress to obtain a faunal list of the gastropods for purposes of comparison" are not listed in the *Bibliography of North American Geology* for 1935–1951. In other words, documentation of dwarfism has apparently not been published while the undocumented published inferences have become part of the literature.

Boni (1940: 341–428) reported on a dwarf Triassic fauna. He found no specimen exceeding 3.0 mm. in greatest dimension, few exceeding 2.0 mm., and the lower limit for the fauna was below 0.5 mm. The fauna consisted of four species of crinoids, four species of echinoids, one of brachiopods, six of pelecypods, 29 species of gastropods, one or two of cephalopods, and one fish species. The earlier paper (1940) which figures and describes the fauna provides the usual data with no particular documentation regarding dwarfism. The later paper (1942) is considered a "contribution to the paleobiology of dwarfism." While it does not provide the documentation relative to dwarfism which is missing in the earlier paper, it does contain a review of the possible ecological factors that might have influence on growth. Obviously, without the essential but missing data, no independent determination can be made as to the occurrence or non-occurrence of dwarfism in this fauna.

Kühn (1936: 255–268) described a middle Miocene coralline-bryozoan fauna and Kutassy (1930: 194–204) described a predominantly molluscan middle Miocene fauna. Both authors considered probable causes of dwarfism but neither provided the necessary documentation to allow the reader to evaluate the conclusions in light of the data.

A diminutive fauna was described from the Ordovician Shakopee dolomite at Cannon Falls, Minnesota (Stauffer, 1937: 55–66; Stauffer and Thiel, 1941: 62–65). The fossils were found in cherty dolomite "where the chert is oolitic, it disintegrates readily and has been found to contain numerous specimens of a diminutive molluscan fauna." The observation was made (idem, 1937) that since no fragment could be considered a large individual, the fauna "may . . . be said to be a diminutive or depauperate fauna whose individuals may have existed elsewhere in more normal size." Other than these remarks, systematic documentation necessary for the determination of depauperization is lacking. The writer had an opportunity to examine this fauna and observed that round oolites filled the opercula of gastropods (*Ceratopea pygmaea*) and a specimen of *Raphistoma shakopeensis* having largest maximum diameter. One specimen each of *Lophospira vetusta* and *Lophospira perelegans* had apertures full of round white cherty oolites which also filled the exposed camerae in some orthoceratids. Some of the larger oolites had approximately the same maximum diameter as some of the smaller gastropods. The evidence seems to indicate that this was a pebble-necrocoenosis rather than depauperate

fauna. The very mode of formation of oolites certainly involves some rolling movement on the bottom and selective sorting of comparable grade sizes is to be expected. The occurrence of specimens of obviously larger dimensions than the rest of the fauna such as *Cameroceras inopinatum* probably indicates that such specimens lay on the bottom in the region to which selective sorting brought the "diminutive" forms and the oolites. The fragment of a free cheek of the trilobite *Entomaspis* found in this fauna recalls to mind another occurrence of trilobite molt fragments in association with oolites (Tasch, 1951: 275–306). This was obviously the result of selective bottom sorting.

We may consider two faunas which Shimer (1908) referred to as dwarfed. These include the Mississippian Windsor fauna of Canada and the Tertiary species of *Planorbis* at Steinheim. Specifically considering the question of dwarfism of the Windsor fauna, Bell (1929: 64) observed (1) units of the fauna are not compared with specifically identical units from more favored localities, (2) in the Maxner and Miller limestone, great numbers of immature individuals are associated with adults, (3) the adults, compared with members from identical or closely allied species from the Avonian of the British Isles, do not show conspicuous signs of dwarfism (*Composita windsorensis* and *Productus lyelli* and its allies are equivalent in size to British relatives), (4) the small gastropods compare with the Scottish gastropods discussed by Donald (1898). Donald observed that many of the Scottish Carboniferous gastropods were of much smaller size than their representatives in England and Belgium. Difference in physical conditions prevailing in the two areas was suggested as a probable explanation. However, Bell (idem: 64) stated that "the Scottish specimens are frequently abnormally preserved, with the protoconchs still intact, which is suggestive of very slight current action and of a youthful demise rather than distinct dwarfing."

Documentation is not provided by any of the writers quoted above. Bell appears to have touched the heart of the matter in stressing the abundance of juvenile growth stages and in expressing doubts as to the presence of dwarfed adults.

Hyatt (1880) arranged *Planorbis* species into progressive and retrogressive series and subseries. The retrogressive subseries were stated to be distorted by disease or decrease in size. He attributed this condition to unfavorable conditions in Steinheim Lake. He also postulated the long since discarded concept of inheritance of acquired characteristics (idem: 15). When one studies the faunal list of retrogressive species by formations in conjunction with the geological sections for the Upper Period at Steinheim (idem: 97–99 and 51), it becomes clear that most of these species ranged throughout much of the column, through beds of varying lithologies but mainly alternating beds of shell sand and limestone. They occurred below and above the one-inch beds of clay containing abundant fossil fish but not in these beds. The time of the catastrophic mass death of fish in Steinheim Lake, was no doubt as Hyatt realized, a time of extremely unfavorable conditions, undoubtedly highly toxic. This, however, was the only place in the column where anything but normal conditions were indicated by the lithology and contained fauna. If dwarfism did occur in Hyatt's retrogressive series, it has still to be demonstrated.

Thus, at least three of Shimer's "dwarf faunas," the Guelph, the Windsor, and the Steinheim Lake faunas have been shown to be so inconclusively "dwarf" that reference to them as "dwarf faunas" can be suspended until adequate evidence is available.

In a paper on "Diagenesis of the Clinton Hematite Ores of New York," Alling (1947: 991–1081) referred to an unpublished paper by Winnie McGlamery (1931) on the "Dwarf Fauna of the Furnace Ore at Rochester." The latter paper was based on collections of fragments of the bryozoan *Helopora fragilis* from the iron ores. Sizes averaged 5.0–6.0 mm. long; 0.5–0.7 mm. in diameter. After death of the organism, the bryozoans fell to the bottom of a shallow sea where they were rolled by waves and rounded and reduced in size. Bryozoans of the above-named species form the nuclei of iron oolites (idem: 1004, fig. 5). Many

specimens of the above bryozoan are reported from the base of the Reynales limestone from Lockport, New York—the horizon of the Furnaceville ore—which itself contains no hematite. These bryozoans are a little larger than those of the ore.

Alling pointed out that in the McGlammery study the microscopic measurements made on cross sections "are not significant" because she did not discount the additions in size due to oolitic coatings. The latter author stressed biologic causes for the reduction in size, i.e., dwarfing. Alling, having remeasured the thin sections and discounted the oolitic accretions, observed that several causes could account for the actual reduction in size, including: wave wear, chemical solution, as well as biologic dwarfing. He finally concluded that 20% of the reduction in size of the hematitic as contrasted with the non-hematitic bryozoans was probably due to biologic causes. To account for this reduction, biologic dwarfing "by salt" and "by iron" was postulated.

Is the 20% reduction in size due to biologic dwarfing? The fact that the hematitic Furnaceville bryozoans occur at the same horizon as the non-hematitic "unreduced" bryozoans, immediately suggests that we have here a normal size distribution over part of a species geographic range. Reductions greater than 20% are known in such distributions (cf. Ingram, 1951: 14–15, table I). The next thing we need to know of the 63 specimens measured and compared, is what growth stages are represented. Reduction in size could also be accounted for by difference in growth stages represented in fossils from the hematitic and non-hematitic localities. There is a sufficient amount of evidence to favor the interpretation that there is a direct correlation between size and salinity and that typically marine "invertebrates in less salty water usually average smaller than those of the same species in higher salinities" (Gunter, 1945: 55–56). This is one of the factors to be anticipated in a given marine invertebrate species range. Alling (idem: 1004) postulated a reduction in size of the bryozoan species discussed above as *due to* "increase of salinity," the reverse of what we might expect[3]. Based on the published information, it therefore seems unlikely that the 20% reduction in size in *Helopora fragilis* can be accounted for by (a) biologic dwarfing, and (b) increase in salinity.

A marcasite fauna in the Ludlowville formation of western New York was recently figured and described (Fisher, 1951: 365–371). The fauna is reported to be characterized by two conditions: occurrence of dwarfed adults and occurrence of a diminutive but not a dwarfed fauna due to some selective action that has destroyed the larger forms. The latter condition is said to predominate. In these terms, this fauna may be described as a diminutive fauna containing some dwarfed adults. The author briefly considers morphologic criteria of stage growth for brachiopods, cephalopods, and pelecypods, but concludes "it was found that a superior method of distinguishing dwarfs was a comparison of fossils in question with the same species in adjacent formations where more favorable environmental conditions were suitable to normal growth" (idem: 367). True dwarfs among the fauna are stated to be the pelecypods, the single blastoid, some, but not all of the cephalopods and gastropods. The diminutive forms are attributed to abnormal environmental conditions and the growth inhibiting agent, either the high concenconcentration of H_2S or Fe. It is further observed that "both the size and quantity of individuals will be considerably reduced should the pH decrease" which condition is brought about by increase in H_2S.

This example of dwarfism is inadequately documented despite the contribution the study makes to stratigraphic and faunal relationships. The writer had an opportunity to examine this fauna. It appears to fall into two major grade sizes: brachiopods, small orthoceratid fragments, and a gastropod species in the 8–4 mm. grade size, and all other components greater than 8.0 mm. The first-named grade size apparently denotes a pebble-necrocoenosis. This could account for the generally diminutive size of all specimens and the exclusion of larger

[3] Cf. discussion of Great Salt Lake fauna, where an exception to this statement is noted.

specimens. The remainder of the fauna in grade sizes greater than 8.0 mm. could have been moved by currents of different competence than elements in the pebble-necrocoenosis. By this approach, variable bottom currents might account for the assemblage as found. The author's "superior method" for distinguishing dwarfs from normal individuals of the same species involved megascopic comparisons with fossils found in "adjacent formations." The detailed results of such comparisons are not given. Neither the dimensions of the so-called dwarf nor the so-called normal specimen of a given species is given. The growth stage of the "normal" specimen is not established by critical evidence. The known upper and lower limits for the normal species size range is not considered. The size of the sample in each case is not stated. Which gastropods and cephalopods are dwarfed is not stated. *Tornoceras uniangulare*, one of the elements of this fauna (five specimens of which were studied by me with a binocular microscope) were definitely not dwarfed and represented juvenile growth stages. Briefly, this is an instance of "reported" but not "established" dwarfism. It is likely that many of the brachiopods, pelecypods and gastropods represent juvenile growth stages.

The fauna of the Phosphoria formation has been given much study by E. B. Branson, Girty, Carl Branson, and A. S. Price. However, for our present purposes, remarks are largely confined to the contribution of Carl Branson (1930). Branson reported that "the oolite phosphate beds are of syngenetic origin for their fauna are typically depauperate" (idem: 14) and in the section near Bull Lake, "the depauperate fauna of Bed Number 27" an oolitic phosphate consists of species of *Spiriferina kentuckyensis, Hustedia phosphoriensis, Nucula poposiensis, N. pulchella, N. montpelierensis, Leda* [= *Nuculana*] *bellistriata, Pustula nevadensis, Plagioglypta canna, Bellerophon depauperata, Pleurotomaria phosphatica*, and *Strophostylus* species. In addition, three fish species are also found with this fauna. The observation was made that as far as presence of fish and the depauperate condition of the fauna is concerned, the fauna of Bed Number 27 is like that of the Lower Phosphate member although generally different in species (idem: 18–19).

Is this a depauperate fauna? One species of this fauna, *Nuculana* (formerly *Leda*) *bellistriata*, was composed, most probably, of juveniles only (See Part I, Table IV). The Wind River forms of *Nucula montpelierensis* were said to vary in size, most of them being smaller than those from Montpelier (idem: 42). *Pleurotomaria phosphatica* also showed considerable size variation, ranging from 2–14 mm. in diameter. Only two specimens of *Bellerophon depauperata* were present in the collection. One of these had a greatest dimension of less than 2.0 mm., while the other had a greatest dimension of 4.5 mm. The author observed that this species "is a member of a typically depauperate faunule" (idem: 53). An average adult tooth of *Hamatus phosphoriensis* was 11.0 mm. in greatest dimension while an immature specimen was 6.0 mm. No dimensions were given for *Spiriferina kentuckyensis* which was described as "typical" (idem: 37). An average specimen of *Pustula nevadensis* was 60.0 mm. long and 55.0 mm. wide. The average size of an *adult* specimen of *Hustedia phosphoriensis* was: length, 11.0 mm., width 9.0 mm., height, 7.0 mm.

The published data on the fauna of the oolitic phosphatic Bed Number 27 is wholly inadequate for our present purposes. A "depauperate" fauna cannot be demonstrated to be present in any strata by generalized statements.

The occurrence of a fauna in association with phosphatic oolites immediately suggests that the "apparent" small size is a function of bottom sorting. If we had the major grade size for the entire fauna, this would become more evident. Based on the size ranges given for some of the pelecypods, gastropods, and some fish teeth, at least part of the fauna falls within the major grade 8–4 mm. This part of the fauna was a pebble-necrocoenosis. Larger specimens (*Pustula nevadensis*, for example) may have been swept shoreward by storm-generated wave action. Coquina-type assemblages in the *Pustula* member of the Phosphoria formation in the Wind River and Owl Creek Mountains (idem: 31) suggest this interpretation.

Specimens of *Nucula montpelierensis* were reported to be smaller at Wind River than

at Montpelier. Normal variation within a species geographic range may be involved rather than depauperization of smaller specimens. The reported size variation in many Phosphoria species might also be partially or entirely due to the difference in size range of different growth stages.

From other studies of portions of the Phosphoria fauna (Girty, 1910, Miller and Cline, 1934) there is no indication of depauperization. Taking all published material into account, it seems doubtful that the oolitic phosphate beds and the phosphatic shale beds of the Phosphoria contain a "depauperate" fauna. However, only more adequate data can conclusively resolve the question.

The marine forms found in evaporites have been referred to as "depauperate" (Krumbein and Sloss, 1951: 180). Megascopic marine fossils are reported to be nearly universally absent (Pettijohn, 1949: 357; Twenhofel, 1939:443–471). The salt and gypsum deposits of Europe, particularly the Tertiary deposits have yielded a wide range of terrestrial fossils including such things as, beetles, dragonfly larvae, birds' tracks and eggs, the terrestrial snail, *Helix*, crocodiles, turtles, large frogs, rodents, fresh water fish, and various kinds of floral remains, such as leaves, wood, etc. (Walther, 1903: 211–217).

The crustacean, *Artemia gracilis*, a brine shrimp abounds in the Great Salt Lake as their fecal pellets indicate. These form the most important part of the sediment covering about one thousand acres and amounting to greater than one-to-two million tons (Eardley, 1938). Jensen (1918: 18–25) experimented with this species, the average male length being 8–10 mm., the average female length being 10–12 mm. He placed eggs in different concentrations of salt water. In all concentrations with specific gravity between distilled water (1.000) and normal lake water (1.109) normal development resulted and nauplii emerged. In a solution with specific gravity higher (1.130) than that of normal lake water, eggs developed into nauplii slowly. This may be interpreted as growth retardation. In still higher concentrations, no nauplii emerged. Apparently, growth was inhibited. Yet these eggs were fertile for when they were transferred to less dense solutions, they hatched readily.

Pack (1919: 273–276) experimented with two protozoan ciliates from the Great Salt Lake and reported the following size variations due to alterations in salinity.

	Density of Solution (Specific Gravity)	Length (mm.)	Diameter (mm.)
Uroleptus packii	1.110	.07	.025
	1.040	.11	.030
Prorodon utahensis	1.110	.06	.023
	1.040	.08	.027

He also noted that like changes were observed in other protozoans of which five to six species are present in the Great Salt Lake. Further, that "the physiology and reproductive processes were accomplished in less time in less dense (i.e., less saline) solutions" (idem: 276).

The findings of Jensen and Pack indicate that in the normal salinity of the Great Salt Lake the abundant crustacean, *Artemia*, and the protozoans show normal development as far as body size is expressive of such development. Thus, no permanent retardation of growth and hence no depauperization appears to obtain in this basin where an evaporite is in the making. Secondly, salinity slightly above the normal amount for the Great Salt Lake definitely retards growth. As shown below, a condition of enhanced salinity occurs seasonally. Still higher salinities inhibit all growth. Both of these effects can be overcome by removal of the inhibitive factor, i.e., removal of eggs or nauplii to less dense solutions.

It is of some importance to observe that the salinity of the Great Salt Lake varies inversely as the volume. On September 5, 1934, for example, a considerable lowering of lake level caused encrustation of the bottom with a one-to-six inch thick layer of coarsely crystalline halite (Eardley, idem: 1319; 1322). At such times (times of annual evaporation during June through November) retardation or more likely cessation of growth of *Artemia* eggs and protozoan cysts may prevail. However, as tributary streams replenish the volume during the annual spring discharge into the lake, conditions of life would again return

to normal. In turn, those eggs and cysts that had weathered increased salinity in a quiescent state would resume normal growth.

In general, marine invertebrates found enclosed in evaporites are thought not to have been indigenous to the area—high salinity acting as an ecological fence—but rather to have been swept in by wave action. As for the flora enclosed in evaporites, only five species of the blue-green algae, *Aphanothece*, were found to be normal to the Great Salt Lake. On the other hand, none of the 62 species of diatoms in the bottom clays of the Great Salt Lake were established in the brine itself but rather were found to live and reproduce in springs, creeks, and marshes tributary to the lake (Patrick, 1936: 157–166; and in Eardley, op. cit.: 1330–1332).

A discussion of barred basins (Woolnough, 1937: 1101–1156) makes reference to the Kara Bougas Gulf on the eastern border of the Caspian Sea. In this gulf, large numbers of fish and other organisms are killed by the saline waters (a sulphate-chloride bittern) and driven ashore. Gypsum and Glauber salt are presently being precipitated (Kuenen, 1951: 45). *Cardium edule* was reported to occur in great numbers on the shore of the gulf. This form apparently abounded in the area before it reached the stage of calcium sulphate deposition (Grabau, 1913: 384). No information is available on the size of these pelecypods as compared to the usual size for the species.

Bitumen associated with evaporites is present as laminae in anhydrite, inclusions in salt crystals, or disseminated in fetid brown dolomites associated with evaporites. It is thought that this bituminous matter is the organic residue of planktonic organisms swept in from the open sea into a gulf or salt sea (Pettijohn, idem: 357). In other words, the occurrence of planktonic organisms in evaporites appears to have been much greater than the fossil record indicates. It is unlikely that such inswept swarms experienced any considerable period of growth in the new environment. It is more likely that the catastrophic death of such swarms occurred shortly after the sudden change of living environments.

One of the rare exceptions to the general rule that evaporites are completely unfossiliferous (*völlig fossilfrei*) appears to be the Miocene salt deposits in Wieliczka, Galicia. Here, in addition to a terrestrial flora and fauna of the type mentioned above, small marine mussels and worms occur in great abundance. These were undeveloped larval forms, that is, plankton swarms that were driven into the saline environment only to be destroyed (Walther, idem).

The above examples and discussion suggest that forms referred to as depauperate in other evaporite deposits were probably juveniles. These were not stunted in their growth "by salt" but killed by saline toxicity while in the immature stages of growth. As for the fauna of the Great Salt Lake, the published information reviewed above does not indicate permanent depauperization although temporary retardation of growth may prevail during the annual evaporation (for further discussion of salinity as a factor in size variation, see below).

Two studies consider the specific problem of the relationship of changes in lithofacies with changes in size within a given fossil species (Reuter, 1907: 9–134; Price, 1920: 544–551). Reuter figures three specimens of *Macrocephalites tumidus* Rein. These specimens are from three different facies (Upper Brown Jurassic of the French Alps) respectively, limestone, phosphate, and pyrite. The limestone specimen is largest and came from the *Macrocephalites* oolite from Troschenreuth. The next specimen in size was composed of phosphatic limestone and came from the type rocks near Busbach. The smallest of the three figured specimens came from Ludwag. In his conclusions (idem: 127), the author observes that "facies variation . . . acts in such a way on the fauna" that the ammonites which are large in the limestone become smaller in phosphatic sediments and while still abundant in the pyrite facies, occur there as a stunted fauna (*verkümmerte Fauna*).

Documentation is not provided. We may be dealing with different growth stages as we pass from one facies to another. Critical dimensions for the total available sample are not given so we can not reach the author's conclusion independently. The geographic range of *Macrocephalites tumidus* is not considered. Yet, the differences noted may be

quite normal when placed in context of the size distribution within a species range. Before decrease in size due to phosphate or dwarfism due to iron can be established, all other possibilities must be systematically examined and eliminated based on sound evidence.

Price considered the maximum size of West Virginia Derbyas as influenced by sedimentation. Survey collections of all available specimens of *Derbya crassa* and *D. robusta* from strata of Pennsylvanian age in West Virginia, 24 collections in all, were used. This involved about 200 specimens. Price measured the width of the shells and arranged them in order of increasing width at the same time noting the character of the matrix. When this was done, it appeared that the shells fell roughly but distinctly into three groups. Group one contained shells of less than average size for the species *D. crassa* and the sediment for this group was black carbonaceous and bituminous shale and limestone; group two, shells of the average-to-large size for *D. crassa* and smaller examples of *D. robusta*. The sediment for this group included chiefly the more calcareous or sandy dark shale and limestone and light-brown and gray sandy shales and sandstones. The third group consisted of larger shells of *crassa* and small-to-large sizes of *robusta*. The sediment for this group included light-colored shales without appreciable amounts of sand grains as well as purer, light-colored, argillaceous limestones.

The criteria Price employed included the following: reference to the upper size limit for a species; reliance on actual size as a determinant of growth stage (idem: 548–549), reference to the "average size" for a species against which sample studied was compared. The latter led him to conclude that the uniformly small shells from black sediments represented "a distinctly dwarfed condition" (idem: 549).

The author pointed out that "larger shells have been obtained from dark sediments at two localities." This was interpreted to indicate the introduction of factors which offset the unfavorable factors accompanying the black sediment. Also, none of the black rocks were found to be noticeably rich in metallic sulphide.

Obviously, a study of this type requires that growth stages be established based on morphologic criteria. Secondly, one cannot lump together two species even if, as with *Derbya crassa* and *Derbya robusta*, they have been interpreted as forming a continuous morphological series. Although a figure is given on which the relationships are plotted, the raw data are not given. Black shale faunas have very often been reported to be "depauperate" or "dwarf" but this fact does not appear to have been documented by an actual series of measurements, together with the locality and sediment. The actual size of a specimen might be related to its growth stage but is not necessarily so. Thus, for example, some juveniles of *Imitoceras* were shown to be larger than some dwarfed adults (see Part I, figure 1). On the basis of the approach used by Price, we would conclude that the juveniles were adults being larger and the dwarfs, juveniles, being smaller. The "average size" for a species is a very misleading figure (Simpson and Roe, 1939: 103–104). The upper size limit for a species, if more meaningful, is so only when growth stages have been established. The weakness in Price's approach can best be pointed up by noting that in group two, while *D. crassa* shells range from average-to-large size, in the same type of sediments, specimens of *D. robusta* consist of smaller examples only. Based on his general interpretation, we could say that *robusta* species are dwarfed in comparison to *crassa* species in the same sediments. This introduces the factor of selective dwarfing in the same environment and also the factor of multiple examples of dwarfism irrespective of lithofacies. Group three presents the same anomaly when the two species are considered.

To tackle the above problem adequately, one would have to know the size distribution of associated fossils found in the same facies so that the major grade size for a facies could be derived. In addition, as shown for *Crurithyris* (Part I, figure 3, and by Percival, 1944), it would be more useful to obtain distribution curves for length as well as for width.

The discussions of Reuter and Price are too inadequately documented to contribute to the general problem of dwarfism.

Generalized statements similar to Reu-

ter's may be found in Dacqué (1915: 423–424 and fig. 75; 1926: 150, footnote 1 and fig. 20, page 163). He observed that in the Upper Cretaceous, reef-building rudistids, corals, actaeonellids, and Nerineididae, as well as large Foraminifera typify the Mediterranean Equatorial belt "and do not go over a certain limit which generally coincides with Alpine Tethys." Furthermore, he noted that to the north and south of the belt, rudistid occurrence is sporadic and "these outsiders are extraordinarily small and have remained dwarfed and isolated." The author is quite specific that these forms are true dwarfs (*Krüppenformen*). Although references are made to the writings of Gregory and Reuter, and to Grabau, whose sources of information on this subject were secondary, as well as to R. Wegner's discovery of large rudistid shells in the North German Cretaceous, no reference is made to published documentation for the use of the designation "*Krüppenformen*" in the above-named example. With more complete information, this example might turn out to be an instance of a normal distribution within a species geographic range.

Summary of published information in Class I.—Class I statements are generally based on secondary sources or when based on primary sources, are incomplete as pertains to data relating to dwarfism. There is no conclusive evidence of dwarfism in any of the published information on the subject reviewed above. If dwarfed elements occur in any of these faunas, that fact has still to be demonstrated by adequately documented studies.

Class II statements.—Three classic studies will be considered in this section. Fauna of the Salem limestone (Cumings and Beede), the depauperate fauna of the Maquoketa shale (Ladd), and the Tully pyrite fauna (Loomis).

Fauna of the Salem limestone.—The most comprehensive work on the fauna of the Salem limestone is the compilation of all available faunal data, figures and descriptions by Cumings, Beede and collaborators, E. A. Smith and E. B. Branson (1905: 1187 ff.).

The authors stated (idem: 1190) that "the fossils in this limestone in its typical development are characterized by their stunted form and extreme abundance. Many of these species are found in the rocks above or below and are then of normal size, usually several times as large as their representatives found in the Salem limestone. In exceptional cases, at unfavorable locations, the species in this horizon reach nearly or quite normal size."

A semi-littoral or lagoonal origin for the "stunted" fauna was the explanation favored by the authors. They cited as evidence cross-bedding, water-worn fossils, oolites and semi-oolitic character, broadly lenticular occurrence. They suggested that the gastropods and brachiopods indicated shallow water conditions (coral reef or lagoonal) and agitation of water. A similar explanation was offered for anchored bryozoans. The Foraminifera and small ostracods which were "so conspicuous an element of the Salem fauna" were swept in by currents from the open sea (idem: 1199–1200).

A brief review of the systematic descriptions is necessary in order to uncover the methodology employed. *Foraminifera:*[4] One foraminifer, *Endothyra baileyi*, was described. Dimensions not given. *Anthozoa:* Descriptions of 21 coral species were given. While in some instances dimensions were given, in no instance was the following information either to be found in the quoted original description or the author's added remarks: (1) size of sample, (2) percentage of given sample in major size groups, (3) maximum known size range for given genus or species, (4) precise location of fossiliferous beds yielding a given species. *Echinoderma:* Descriptions of 33 species were given. Rarely were size data included. Species were referred to as "small," "robust," "large," "rather large," "above medium size." etc. *Bryozoa:* E. R. Cumings (idem: 1274) noted that those who had gained the impression that the Indiana oolite contains only small dwarfed fossils would be surprised at the many normal beautifully preserved fenestellids and other

[4] E. J. Zeller (cited *in* Lalicker, 1948) reports the occurrence of a giant fauna of both *Endothyra* and *Plectogyra* which make up 85% of the rock (Salem limestone, basal Meramecian of Indiana). He has not yet noted any dwarfed species of these genera in the formation.

bryozoans from the Dark Hollow quarries of Bedford. A further observation was made that "where the stunted fauna comes in, as at Harrodsburg, fenestellid Bryozoa are either absent or in such small fragments as to be nearly unidentifiable. At Harrodsburg small species of *Rhombopora* are fairly common." Descriptions were given for 41 species or new varieties. Many of the descriptions gave numerical data. However, the same type of data noted as being absent in the descriptions of the Anthozoa was lacking here.

Similar limitation of numerical and related data is found in descriptions of pelecypods, brachiopods, gastropods, cephalopods, and trilobites. Cloud (1948) states that in the Salem limestone it is a fact that some of the very small brachiopods show beak features of adult shells. This, taken alone, does not establish these small adults as dwarfs.

With one possible exception, mentioned below, the raw data made available in the Cumings-Beede compilation do not permit an independent evaluation leading to a definite answer to the question, "Does this fauna contain true dwarfs?"

The three main criteria used by the authors in determination of dwarfism are, (1) generally observed small size, (b) occurrence of the same species found "dwarfed" in the Salem, in beds above and below it, (3) or, in certain facies at the same horizon as the Salem limestone.

The paper by E. A. Smith on the "Development and Variation of *Pentremites conoideus*" (idem: 1219–1242) which forms part of the Cumings-Beede report on the Salem limestone fauna, provides the very type of documentation lacking for the rest of the fauna.

Of 5,700 available specimens, 735 were measured by Miss Smith. Of these, 276 specimens were from the Old Cleveland Quarry near Harrodsburg, Indiana in the upper part of the Salem limestone. Hereafter this sample will be referred to as "Harrodsburg." Another 240 specimens came from the upper part of the Harrodsburg limestone (the formation below the Salem), hereafter referred to as "Pentremite Hollow."

The number of poral pieces was taken as the criterion to determine age. Thus, all specimens with 8–12 poral pieces were put in one age group. Then the different characters of this group were studied. Based on Smith's figures (idem: 1238), I have summarized and analyzed the pertinent data in two tables, Table 8 and Table 9, below.

From the data provided in Tables 8 and 9, but not as analyzed in these tables, Smith concluded that the fossils from Harrodsburg are dwarfed forms while those from Pentremite Hollow are normally developed. Table 8 shows that only 63% of the Harrodsburg specimens had the same number of poral pieces. Hence, by the author's definition, these were of the same age. For the remainder (37%), at this locality, no comparative measurements could be made since they differed in the number of poral pieces and thus, no age determinations could be made. At Pentremite Hollow, 57% of the

TABLE 8.—ANALYTICAL COMPARISON OF NUMBER OF PORAL PIECES IN *Pentremites* AT TWO LOCALITIES

	Locality			
	Harrodsburg		Pentremite Hollow	
	N	Per cent	N	Per cent
1. Total number of specimens	276	100.0	240	100.0
2. Specimens with the same number of poral pieces (hence of same age by definition)	173	63.0	104	43.0
3. Specimens with smaller number of poral pieces than in (2) above	71	26.0	33	14.0
4. Specimens with larger number of poral pieces than in (2) above	32	11.0	103	43.0

TABLE 9.—ANALYTICAL COMPARISONS OF AVERAGE MEASUREMENTS OF *Pentremites* AT TWO LOCALITIES IRRESPECTIVE OF AGE

Character Measured	Number of sets, out of 21 sets of comparisons of *Pentremites* with same number of poral pieces	Average Measurement[a]	
		Harrodsburg (mm.)	Pentremite Hollow (mm.)
1. Absolute length of ambulacral area	13	5.80	5.91
2. Absolute length of base	19	3.57	3.83
3. Relative length of ambulacral area	17[b]	1.62	1.54
4. Angle between ambulacra and radius of base	20	(115°)	(110°)
5. Length	10[c]	7.59	7.28
6. Breadth	21	5.67	6.40
7. Length/Breadth	20	1.33	1.15

[a] All figures in these two columns, except Item 4 are to be read, 5.80 plus, 3.57 plus, etc.
[b] Plus one identical.
[c] Plus two identical.

specimens fall into the category of undeterminable age.

The author did not restrict her comparison to only those specimens at both localities of the same age. When this is done, one does not reach the conclusion that the Pentremite Hollow specimens are normal while the Harrodsburg specimens are dwarfed. Actually, when the data are analyzed as in Table 9, irrespective of age, the Harrodsburg specimens show a greater relative length of ambulacral area, a greater angle between ambulacra and radius of base, a greater length, and a greater ratio of length to breadth than the so-called "normal" Pentremite Hollow specimens. It may be further noted from Table 9 that where the Pentremite Hollow specimens have a larger dimension, the measured difference is never very great. Certainly, a difference of a few tenths of a millimeter in but three out of seven critical dimensions cannot be taken as diagnostic of normalcy. Such difference is most likely within the range of the measuring error.

For the fauna of the Salem limestone as a whole, it appears quite clear that bryozoans and Foraminifera are certainly of normal or greater than normal size. Dwarfing of the cystoid *Pentremites* at Harrodsburg has not been established. Insufficient documentation prevents determination from the published material as to the dwarfism or normalcy of the rest of the fauna. Accordingly, pending such documentation, further reference to a stunted or dwarfed Salem fauna may be considered a statement unsupported by acceptable or definitive evidence.

Fauna of the Maquoketa shale.—There have been numerous papers devoted to the fauna of the Maquoketa shale (Ladd, 1924, 1925), brachiopods (Bradley, 1921; Wang, 1949), trilobites (Slocum, 1913), ostracods (Spivey, 1939; Keenan, 1951, Bolin, 1952), cephalopods (Foerste, 1936; Miller and Youngquist, 1949). Nevertheless, treatment of the so-called depauperate fauna in any detail is to be found only in Ladd's paper.

Ladd originally traced the "depauperate zone" in Jackson County, Iowa and gave a list of fossils from this zone which were found at three localities: Bellevue, Tete de Mort, and Dubuque, Iowa (1924: 26). The most important observation made in this preliminary study was that as a "general rule" the depauperate zone fossils tend to be larger towards the northern as compared to the southern localities (idem: 34). The decrease in size of fossils towards the southern localities so impressed the author, that he designated the fauna at Bellevue as "depauperized depauperate" when compared to the forms at Dubuque. He also observed that *Orthoceras sociale* of "normal size" (18.0 mm. in greatest diameter) occurred in abundance at Tete de Mort town-

ship and Dubuque together with associated forms of "subnormal size." At Bellevue, the average diameter of orthoceratids was 3.0 mm. On the occurrence of the other normal sized fauna in the "depauperate zone" Ladd reported a large *Lingula* fragment (10.0 mm. across) found near Bellevue. Spivey's study of the Maquoketa ostracods indicates that they are "normal in size and perhaps slightly larger than average." A recent study of the "depauperate zone" ostracods in northeastern Iowa (Bolin, personal communication, 1952) indicated that the ostracods from this zone, though common, "were quite limited in variety of species. All specimens were rather small as ostracods go, but not extremely so." The ostracods are "distinctly but not abnormally small." Scott (1948: 65), referring to Spivey's study, commented that all ostracods that did not meet with some unfortunate accident attained the full ostracodal maturation of 1.00 mm. length.

Keenan (op. cit.) studied Maquoketa ostracods from the Castlewood, Missouri, conglomerate. He doubts that this zone correlates with Ladd's "depauperate zone." Both are similar in being phosphatic, pyritic, and fossiliferous. Normal ostracods occurred together with graptolites, conodonts, etc. Large fossils are absent (personal communication, 1952).

Thus, every study of Maquoketa ostracods, whether or not in the "depauperate zone" shows that only normal sized ostracods are present.

We may, therefore, place the "depauperate zone" ostracods alongside of lingulid brachiopods and orthoceratids as "normal" components of the Maquoketa fauna.

In Ladd's preliminary study, the growth stages represented at Dubuque and Bellevue are not indicated. Thus, we cannot tell if the average diameter of 3.0 mm. for orthoceratids at Bellevue in contrast to "normal size" at Dubuque indicates abnormality or a difference between juveniles and adults. We do not know whether the size differences noted at the two localities are "real" or "apparent" for any gastropod, pteropod or pelecypod. The very use of the term "depauperized depauperate" indicates a size range which could very well designate different growth stages. Critical dimensions are not given. Thus, for *Dalmanella* cf. *hamburgensis* we have the general statement that "Bellevue specimens average smaller than those figured from Minnesota" and we are given the size of one large specimen. With a more complete tabulation for any given species, graphic analysis would be possible.

In the expanded study of the Maquoketa (Ladd, 1925) several additional points were raised and new data, important for the present discussion given. Nevertheless, documentation relative to depauperization was still inadequate, although excellent lithologic and paleoecologic data were provided.

The depauperate fauna of the basal Maquoketa was reported to consist of 52 species "which rarely exceed a quarter of an inch in diameter." The observation was made that these species were not dwarfs "but make a group of small animals none of which ever grew any larger" (idem, 1925: 86). As mentioned previously in the discussion of "Terminology," a fauna of this type is a normal fauna. However, Ladd did not intend to state that this fauna was normal. Elsewhere in his consideration of causes of dwarfism he makes this clear. Then we must restate the above quotation as follows: *the fauna did consist of small animals some or all of which grew larger at different localities.*

In the absence of data on growth stages even this modified statement remains somewhat ambiguous.

In terms of major grade size (6.3 mm.) this fauna was more likely a pebble-necrocoenosis than a depauperate fauna. However, other data should be considered before reaching any conclusion.

The author (Ladd, idem: 211) stressed two aspects of the lithology of the depauperate zone: the occurrence of pyrite and of phosphate. The former, he held, was probably secondary and hence of no significance as a probable cause of dwarfism. The phosphate he thought to be primary and he observed that the depauperate zone "is always phosphatic, i.e., literally the whole zone, including fossils, matrix, pellets and large pebbles." The upper Galena layers and shales overlying the depauperate zone (except at Graf, Iowa) rarely show a trace of phosphate, hence, the author suggested that "*the presence of phosphate in the Maquoketa sea may be related to depauperization.*" (Italics mine.)

Fragments of the graptolite, *Diplograptus peosta* Hall were reported in the depauperate zone of both the northwest and southwest areas (idem: 112, 136). This is of paleoecological interest since they are abundant at higher levels within the Maquoketa (base of *Isotelus* bed). The wide distribution of three different species of a probable conodont which Ladd observed are usually present though never abundant may partly account for the widespread distribution of phosphate in the depauperate beds. In other words, these probable conodonts may not have been abundant because of chemical dissolution contributing phosphate to the sediments. Although sparse as fossils, phosphatic lingulid brachiopods could also have contributed phosphate to the sediments (cf. Branson, 1933: 284; Rankama and Sahama, 1950: 588–589).

A single specimen, *Cycloceras* cf. *clorus baffinense* (Schuchert) (equals *Spyroceras baffinense* Schuchert) was described from the depauperate zone at Tete de Mort township (1925: 194). The individual segments of that specimen measured 3–4 mm. in length and averaged 13 mm. in width. The writer was able to measure Schuchert's three figured syntypes (USNM 28192) as well as the Miller-Youngquist collections (hypotypes) from Baffin Island. The results are summarized in Table 10.

sion that for the depauperate zone, fossils tend to increase in size to the northern localities. It also makes it clear that depauperate zone fossils did grow to larger sizes elsewhere outside of the zone. The difference in latitude of Iowa and Baffin Island (Frobisher Bay) is 28°. Was this an instance of an increase in size with higher latitudes? The horizon from which *Spyroceras baffinense* came (A. K. Miller, personal communication, 1952), is quite close to the Maquoketa in age, being a little older than the latter. For the above finding to be conclusive, it would have to be shown that the Baffin Island and Maquoketa horizons were of equivalent age. Nevertheless, the relationships in size distribution indicated through a geologically short lapse of time might also suggest the distribution to be expected when fossils from widely separated horizons more closely equivalent in age are involved.

Although data on dimensions of specimens are incomplete, most species appear to show a size decrease to the south. Two observations strengthen the interpretation that this may be the result of a normal size distribution: (1) the above discussion of *Spyroceras baffinense*, and (2) Ladd's observation that Minnesota specimens of the brachiopod *Dalmanella* cf. *hamburgensis* were larger than those at Bellevue, Iowa.

TABLE 10.—MEASUREMENT OF INDIVIDUAL SEGMENTS OF *Spyroceras baffinense* SCHUCHERT

Average Length (mm.)	Number of Specimens N = 19	Per cent	Average Width (mm.)	Number of Specimens N = 19	Per cent
2–4	5	26.0	13[a]	7	36.0
4–6	9		14–15	6	
7–8	3	74.0	19–24	5	64.0
10[b]	2		25–26	1	

[a] Less than 13.
[b] Greater than 10.

Table 10 indicates that of all known Baffin Island specimens, 26.0% had an average length and 36.0% an average width in the range of the depauperate zone specimen. However, 74.0% and 64.0% respectively, had a greater average length and width per segment. While not conclusive, this finding extends Ladd's general conclu-

Thus, the smaller end of the species size range for at least several Maquoketa species would be found in the southern parts of the depauperate zone.

The immediate question then, is, "How can we account in this way for an assemblage of 52 distinct species with an upper size limit of a quarter-of-an inch in diam-

eter?" The résumé of the lithology of the depauperate zone indicates that minute pellets and pebbles and depauperate fossils tend to concentrate within the beds. This could be accounted for by selective bottom sorting of comparable size grades. Phosphatic pebbles or clay pellets would both have been shaped by some bottom action such as rolling on the bottom. The fact that irrespective of species, the major grade falls within pebble size for all fossils, makes it reasonable to conclude that the fauna was a pebble-necrocoenosis. Thus, though different species occupied different ecological niches in the Maquoketa sea and on the sea bottom, at death, current sorting brought them together as though they had all occupied the same or contiguous niches. As will be shown in a later section, for living marine invertebrates, it is a general rule that species increase in size towards higher latitudes. A factor of this kind could, at least in part, account for the size distribution of the depauperate fossils at different localities.

Certainly nothing conclusive can be said about the fauna of the depauperate zone until data on growth stages become available. Still, the above discussion brings out the fact that *the assemblage as actually uncovered from the rocks can be explained in ways that exclude depauperization.*

Can a concentration of phosphate cause depauperization? It is true that depauperate faunas or forms have been reported from such beds before (Reuter, 1907; Ball, 1935; Branson, 1930; Pettijohn, 1949), although in no case is there any documentation adequate to prove depauperization. Then too, there is a form of phosphorus, white phosphorus, that is lethal in doses of 0.15 grams and causes necrosis of the bones (Pauling, 1938: 405). However, this form condenses from tetratomic phosphorus vapor at 280.5°C. On the other hand, phosphorus occurs in the sea in three forms, phosphate in solution (calcium phosphate), as organic compounds, and in plants, animals, and detritus (Harvey, 1942: 227). The first two forms have not been reported to be physiologically toxic. The third of the three forms is obviously non-toxic. The main mineral constituent of bones and teeth of animals is hydroxyapatite, which, upon death, would be available for redistribution as calcium phosphate upon loss of the hydroxyl ion. Other phosphorus compounds, such as phosphine, are highly poisonous but special circumstances are necessary for their formation—circumstances not likely to occur in the sea. In addition, as will be shown later for iron whose physiologically active form is ionic iron (pp. 427 ff), so for phosphorus the physiologically active form that is significantly involved in metabolic reactions of living organisms consists of complex organic compounds of phosphorus (Pauling, p. 404; Meyerhof, 1931: 682–686). Such compounds may be, in part, the source of the phosphorus used by phytoplankton (Rankama and Sahama, 1950: 588). Yet, although size variation in diatoms, for example, has been attributed to temperature changes (Wimpenny, 1936; cf. Garstang, 1937; Harvey, 1933), no change of this kind has been attributed to the physiologically active form of phosphorus. It is also of importance to note that the amount of phosphorus in organic compounds in solution in sea water or in living animals or detritus undergoes seasonal reduction (Harvey, 1942).

The likelihood is, that regardless of the total concentration of calcium phosphate in sea water, only that phosphorus combined in complex organic compounds will influence organisms. A side effect of such compounds in sea water would be buffer-action tending to prevent any sizeable or sudden changes in pH (Pauling, op. cit.: 389–391). Thus, it is unlikely that phosphatic sediments such as are found in the Maquoketa were deposited in an environment subject to wide changes in pH.

A different approach can be taken to this problem. Where is there a great concentration of phosphate in the sea today and how is it affecting marine life? Sea water deeper than a few hundred meters is thought to be saturated with $Ca_3(PO_4)_2$ (Harvey, 1928: 170; Dietz, Emory and Shepard, 1942: 836; Graham and Moberg, 1944: 8). It is doubtful whether any significant quantities of phosphates are consumed below a depth of 75–100 meters although phytoplankton have been found at a depth of 400 meters (Graham and Moberg, idem: 7). This suggests that the major way in which phos-

phate in sea water enters the food chain is via the phytoplankton which consume it at depths of less than 100 meters. What becomes of the great concentration referred to above? One of the two factors in the vertical distribution of phosphate in sea water is the transportation of phosphate at lower levels (subphotic zone) to higher levels (euphotic zone) by vertical circulation. Convective currents, eddies, upwelling of waters are some of the forms of vertical water movements. Replenishment of phosphates in the euphotic zone by upwelling of water from subphotic zones is a well-known phenomenon and related in an important way to commercial fishing operations (Carson, 1951: 146–148). Thus, the majority of marine invertebrates do not appear to come into direct contact with high concentrations of phosphates. The reason appears to be that the phytoplankton serve as their phosphate-storers and these forms, in turn, do not have to go below 100 meters to consume needed phosphorus. However, as Harvey op. cit.: 170) makes clear, about 75 billion tons of phosphate reckoned as P_2O_5 is concentrated below a depth of 100 meters, especially in the low latitudes where restraint of vertical circulation to the surface is imposed by the lesser density of warmer layers above the zone of phosphate concentration. He points out that this quantity of phosphate is lost to the cycle of events "for an almost indefinite period." Following this observation, the logical question is, are any marine invertebrates whose zone of life is this concentrated phosphate zone, depauperate or dwarfed? Drs. H. W. Harvey and William Beebe, to whom this question was put, replied in the negative. In personal communications to the writer, they stated that no published information on this subject is known to them. Based on the information which is available at present, it seems reasonable to conclude that if depauperization or dwarfism in this zone were a common event, it would have become known to some marine biologists by now. By the converse view, it may be observed that the upwelling of phosphate-rich waters from intermediate levels of the sea does not appear to create conditions leading to depauperization of the marine invertebrates at higher levels since this phosphate is consumed by the phytoplankton.

The occurrence of graptolites and of pyrite and much limonite in some beds suggests that reducing conditions probably came to prevail at least locally at certain times. The toxicity thus created may have caused mass death of the invertebrates now represented in the Maquoketa depauperate fauna. Thereafter, having settled on the clay mud bottom, a biological assemblage became transformed into an unsorted array of clastic particles which, after bottom-sorting, occur in the rock record as a pebble-necrocoenosis.

Fauna of the pyrite layer of the Tully limestone.—Loomis (1903), in describing this fauna, observed that "few of the specimens are over 2.0 mm. in diameter *but are adults*" (Italics mine). The fauna consisted of 51 species including Crustacea, Cephalopoda, Lamellibranchiata, Gastropoda, Brachiopoda, Crinoidea. These species were compared with Hamilton "ancestors" from whom they descended. Loomis regarded them as "mutations," that is, "species (that) have arisen under abnormal conditions." The author noted that "the fauna is not uniformly dwarfed, large specimens occurring among the otherwise tiny forms." Further, "the dwarfing agent has totally eliminated the corals; the Brachiopoda are most uniformly and extensively dwarfed; the Lamellibranchiata are much affected; the Gastropoda and Cephalopoda are mostly tiny but also have some medium and occasionally large sized representative, all adults" (idem: 894).

A reader of Loomis' paper cannot determine whether this fauna contains true dwarf elements from the limited data provided. We do not have dimensions of the Hamilton "progenitors" and of the total available sample of Tully pyrite progeny; we do not know, except by report, whether forms said to be adults are true adults, since the specimens involved, and all critical details pertinent to growth stages, are not fully discussed. The major grade size for this fauna is 2.0 mm., hence this is a granule-necrocoenosis. The author indicated that three different size groupings obtained among the gastropods and cephalopods

They were described as "mostly tiny, some medium, and occasionally large-sized representatives." He concluded that regardless of size, however, they were all adults. This remains to be demonstrated. It is most unlikely. Based on the evidence presented in Part I, it would appear that the occasionally large-sized individuals were the adults and all other juveniles. In the oolitic hematite band of the Clinton beds, another formation studied by Loomis at Rochester, New York, he found "these species had an average of about one-third the diameter of the same species in beds above and below it." This, of itself, cannot establish dwarfism as the cause for this size difference. In Part I it was shown that the "Dry shale fauna" consisted largely of juveniles which met catastrophic death due to toxicity. This could readily account for a decrease in size such as Loomis observed in the Clinton beds. It could also account for most, if not all of the Tully pyrite fauna. One of the criteria Loomis used for concluding that the fauna contained adults only was "uniformity of size" among the brachiopods, for example. This suggests something quite different to the writer. Sorting of clastic particles on the sea floor by bottom currents could result in uniformity of size since fossils of similar size offer equivalent resistance to movement (with modifications, of course, due to shape). *Uniformity of size seems more likely to be the result of sedimentary than biological processes where fossil assemblages are concerned. Variation and individual differences seem to be the general biological end whereas in sorting, sieving, etc. the end appears to be uniformity.*

Thus, it becomes clear that the classic example of dwarfing by iron, the Tully pyrite fauna, has not yet been sufficiently documented to establish any of its elements as dwarfs. That such dwarfed elements may be found to be present is not disputed here. Rather, alternative explanations for the small uniform size of this fauna have been suggested.

Summary of published information in Class II.—The three most widely quoted examples of "dwarfed" or "depauperate" faunas are found to be poorly documented for the purposes of establishing dwarfism or depauperization. If there are any dwarfed elements in the Salem or the Tully, or any "depauperate" elements in the Maquoketa, it is still to be demonstrated.

BIOLOGICAL EVIDENCE OF FACTORS AFFECTING GROWTH

The physiological effect of trihydrol in water.—The nature, composition and origin of water has been given much consideration in geologic discussions (Rubey, 1951). However, no attention appears to have been given to the polymeric system of water and the physiological effects of different polymers on marine invertebrates. Water may be regarded as a system of three polymers: monohydrol (steam) H_2O; dihydrol $2H_2O$, which is the main component at ordinary temperature; trihydrol (ice $3H_2O$[5] (Bayliss, 1927; 233 ff; H. T. Barnes, 1928: 1–364; cf. R. C. Miller, 1946). At any temperature there will be a certain relative proportion of all three of these substances.

T. C. Barnes and co-workers (1932a, 1932b, 1933, 1934a, 1934b) conducted a series of experiments on *Spirogyra nitida* and *Euglena gracilis*. In each case they found growth more rapid in cultures rich in trihydrol than in control cultures in monohydrol or dihydrol kept at the same temperatures. Similar findings were reported for the diatom, *Nitzschia closterium* (Harvey, 1933: 273) where growth proceeded more rapidly in water previously frozen and melted. Zo Bell (1934: 460–465) observed an increase in the total number of bacteria and a decrease in the number of predominating species in samples of sea water held at near 0° for a few hours. Hegarty and Rahn (1934: 21–30) found that of three cultures of *E. coli* respectively in condensed steam (monohydrol), normal water (dihydrol) and melted ice (trihydrol), the trihydrol culture showed greatest growth after six hours and after 36 hours. In freshly distilled

[5] Alternative views have been proposed for the structure of water which exclude the trihydrol polymer. However, the important point for the present discussion is that the reported physiological effects of previously frozen water have not been invalidated by later findings. Second, T. C. Barnes (personal communication, 1951) still adheres to the polymer system discussed above.

water, the authors found a *retardation of growth* observing that "it appears necessary for the water to be vaporized and condensed to produce a noticeable retardation in growth." (cf. Locke, 1895). Kesling (1951) found that growth of an algae culture was slightly greater in pond water than in distilled water. This can probably be accounted for by the fact that seasonal freezing of pond water and subsequent melting enriches the water in the trihydrol polymer. Hart (1934: 3–217) expressed the belief that "this factor (newly melted ice) may be an extremely important factor in polar seas." He further noted that "not only melting of ice, but temperature of water is involved in the operation of this factor, low temperatures favoring the persistence of a high proportion of trihydrol. This may be a partial explanation of the poverty of phytoplankton observed during the abnormally warm season 1929–30, and of the fact that the positions of richer diatom hauls showed a closer correlation with low temperatures than any other hydrological feature." T. C. Barnes (personal communication, 1951) writes, "I am convinced by all the evidence that trihydrol stimulates some types of living cells."

Latitudinal variation in size of marine invertebrates.—Information on size distribution of living marine invertebrates is penetratingly summarized and discussed by Wimpenny (1941: 389–425). It appears that for the bulk, though not for all animal forms, there is a tendency for size to increase with latitude. The most common exceptions to this central tendency among marine invertebrates are marine diatoms, massive gastropods, and the huge pelecypod, *Tridacna*, found along tropical coasts, while smaller molluscs are found towards the poles (cf. Forbes, 1859). Larger species of the cirriped, *Balanus*, and the largest hydroids are also reported in warmer seas. Among the vertebrates, fish weighing over a thousand pounds also occur in warmer water (idem: 413). However, it has been observed that "fishes of cold or saline water usually attain a larger size (i.e., have more vertebrae) than do individuals or races of the same species inhabiting warm or brackish water or both" (Hubbs, 1926: 60, cf. Huntsman, 1919: 592). As for marine flora, diatoms are also exceptions to the above-noted tendency.

One of the clearest examples of size variation with latitude in the literature is found in the papers of Odhner (1931: 1–7; 1944: 31–34). He found that for the scaphopod, *Cadulus dalli*, the largest specimens came from the Antarctic waters (variety, *antarcticus*) while in the Patagonian Region (West coast and Magellan Strait) from where the typical form was first recorded, a somewhat smaller size was attained. Reference to a map shows that the smaller size occurs *outside the northern limit of drift ice.* It is also of interest that the Antarctic specimens were obtained from depths of 360 and 400 meters from an argillaceous mud bottom containing pyritic gravel.

Mann (1948: 9–332), on an exploration trip to the South Shetland Islands, Adelaide Island, and Graham Land, all within the mean limits of drift ice, found that the following invertebrates were characterized by giantism (*gigantismo en los invertebrados*): Foraminifera, hydroids, echinoderms, annelids, crustaceans, molluscs, and tunicates. Giant size of invertebrates was listed as one of the 12 characteristic traits of Antarctic life. Comparing individuals of the same growth stage, the length of European species of the anchovy, *Engraulis*, was found by Blackburn to be greater than that of the related Australian species and the growth rate of the former nearly twice as great (1950: 69). Parke (1948: 651–709) found that with an increase of approximately six degrees in latitude, there is a higher rate of frond growth in *Laminaria saccharina* (L.) Lamour throughout the yearly cycle at the more northern of two collecting stations (coasts of Devon and Argyll respectively). The observation has been made that ostracods are smaller in warmer waters at maturity than those living in colder waters (Spjeldnaes, 1951). Witschi (1942: 51–69; 1952) gave the geographic distribution of European frog larvae which live in an aqueous environment and showed that they distributed into three fairly distinct belts according to whether they were sex-differentiated, undifferentiated, or semi-differentiated (bisexual). When these localities were plotted on a glacial map of Europe by the writer, it was found that the undifferentiated larvae were greatest in un-

glaciated areas, differentiated were distinctly confined to glaciated areas, and semi-differentiated occurred on late and maximum glacial margins. Since sex differentiation is related to growth, the present writer suggests that previously frozen water may be a factor in the reported distribution.

While the bulk of the evidence points to verification of the central tendency for increase in size with latitude suggested by Wimpenny, account should be taken of negative evidence. As noted, Wimpenny did take this into account. He called such forms the "minority group." However, other examples occur in the literature that deserve mention. Herrick (1911:352) observed that the rate of growth of lobsters at two localities, Wickford, Rhode Island, and Woods Hole, Massachusetts, was "less in slightly colder water at Woods Hole in the case of artificially hatched and reared young." This might, however, not be the case if fry naturally hatched and reared were involved. Ting Ying (1937: 1–227) found that Recent corals of the same species showed "longer annual growth in warm regions and shorter annual growth in colder regions" (idem: 17). When data given in his paper for *Madreporia imperforata* were tabulated by the writer according to decreasing latitude, it was found that the average annual growth is also greater in lower (warmer) latitudes (idem: 35–57). Murray and Irvine (1889: 81–82) reported that as one approaches the colder water at the poles, "we find only one or two thin shelled pteropods and one or at most two, dwarfed species of pelagic Foraminifera." The dwarfism of these species has not been documented but if they actually do occur this would contrast interestingly with Mann's observations on the giant Foraminifera in the Antarctic. Cushman (personal communication in Lalicker, 1948: 55) pointed out that there is a decreased size in several species from colder waters of the north Pacific Ocean compared with specimens of the same species from tropical waters.

Occurrences in the geologic record are of interest when viewed in light of the central tendency discussed by Wimpenny. In the northern part of its range, Tertiary and Quaternary Pectens are reported to be larger than in the south (Dall *in* Arnold, 1906: 133). A trend of increase in maximum sizes attained in *Belemnitella americana* as one goes from Mississippi northeastward to New Jersey, has been noted (Urey, et al., 1951: 415). Reports of giant Producti and Spirifers and huge specimens of other forms in the geologic record of the northern latitudes are reviewed by Holtedahl (1924: 160–165). The author also pointed out that these were mainly shallow water forms and that in 70°–80° North latitude today such shallow water bodies would "no doubt have been frozen practically to the bottom during winter time." In terms of the present discussion, this would indicate a periodic renewal of trihydrol in such water bodies.

Gregory (op. cit.: 411) maintained that "the fossil faunas of the Arctic seas all show the dwarfing effect of unfavorable conditions when compared to contemporary faunas." This statement is disproven by Holtedahls' review of later evidence.

Flower (1946: 125–126) noted the striking disparity in size between Cincinnati forms (cephalopods, corals, brachiopods) and congeneric species from northern latitudes. Arctic forms such as *Lepidocyclus* ["*Rynchotrema*"] *capax* were characterized by gigantism. This observation corresponds to the evidence presented by Holtedahl and Mann. The apparent size increase at higher latitudes of the Ordovician orthoceratid, *Spyroceras baffinense*, also corresponds to what appears to have been a general trend during the Ordovician (cf. Table 10). Flower attributed size increase at higher latitudes to tropical conditions. Even if such conditions did prevail for a time, annual renewal of trihydrol seems indicated as discussed above. The probable significance of this renewal is considered in the next section.

Trihydrol, latitudinal size variation, and dwarfism.—Dwarfed and giant fossil corals have been reported from the northern latitudes. This anomaly can be explained by the trihydrol theory. Decrease in the proportion of trihydrol in sea water might correlate with the occurrence of dwarfed corals. Seasonal renewal of trihydrol by melt waters of frozen seas or glaciers might correlate with the occurrence of giant corals and other giant forms.

In general, we can correlate with Wim-

penny's central tendency—latitudinal increase in size—periodic addition of trihydrol to the sea by glacial melt waters. In turn, this would favor accelerated growth. Changes in the temperature of the sea at different latitudes can be caused in a number of ways. These include: influx or upwelling of cold or warm currents (cf. Hutchinson, 1951: 734, Paragraph 3, Item 4) or seasonal stratification into distinct water systems of a given water mass (Ishiwada, 1951: 1–4; Marshall, 1933: 126). Certain anomalies in growth reported for marine invertebrates may be explained in this way. Many brackish water faunas previously reported to be depauperate, may be so due to lack of trihydrol and an abundance of the monohydrol polymer. Trihydrol or previously frozen water may accelerate growth of phytoplankton. Thus, if we follow the food chain in the sea (Harvey, 1928: 167), we could explain the giantism noted by Mann in the Antarctica area in the sense that food consumption is naturally a factor in growth. Glacial melt waters are not the only source of trihydrol. Any previously frozen water in lakes, ponds, rivers, bays or elsewhere will be rich in trihydrol. This may account for local anomalies in size distribution within certain fossil species.

The problem of growth is extremely complex and it is doubtful if any single mechanism could explain all associated phenomena or occurrences of size distribution (cf. Weiss, 1949). Nevertheless, by numerous independently accumulated kinds of evidence, trihydrol or previously frozen water appears to be an important factor that can account for some of the puzzling phenomenon observed by marine biologists and paleontologists.

Several explanations for the observed latitudinal size increase have been put forth by different authors: the same amount of organic matter could be more economically supported in cold than in warm habitats (Harvey); low temperature and not food is primarily responsible for increase in size (Coker); the onset of maturity is retarded and a longer time available for somatic growth in these conditions (Hesse; Mann); a sluggish rhythm of living motivated by low temperatures which results in the abundance of organic reserves later utilized in the elaborations of new aggregations of protoplasm and for the interim, in a notable enlargement in size (Mann).

All of the above explanations may ultimately be a function of the proportion of trihydrol in sea water. The exception is low temperature which would be a control of the proportion of trihydrol in sea water.

The sulfhydryl theory and retardation of growth.—F. S. Hammett and coworkers (1931, 1932, 1933, 1934, 1936, 1939) reported results of a series of experiments on marine organisms. These findings all tended to confirm that growth and development is accelerated by sulfhydryl and retarded by its incompletely oxidized derivative, sulfoxide (cf. Chalkley, 1951: 1308). The forms experimented on included: blue-green algae, the marine annellid, *Clymenella torquata*, the hermit crab, *Pagurus longicarpus*, *Obelia*, etc. Dr. Hammett pointed out (1936) that the sulfhydryl group which is universally present, active or potential, in cytoplasm, "is known to be not only essential to and an accelerator of cell increase in number but also *to be a probable partial determinant of the species, specific size differences* in two races of rabbits (and) its concentration in early embryonic cells of essentially the same size is postitively correlated with subsequent animal size—being higher in what is to give rise to giants, lower in dwarf *anlage*— and intermediate in value in that of the mixed strain." (Italics mine.) Sulfoxide was found to decrease the numbers of mitoses in each germ layer derivative in the *Clymenella* experiment. In regeneration experiments with the hermit crab, it was found that "*growth in size* and differentiation as well, is much less when sulfoxide is present" and that in "marine as in land forms, it is possible to stimulate growth or retard growth at will with –SH and its partially oxidized derivative respectively" (Italics mine). These experiments also showed that a salt water milieu does not prevent expression of the reaction (1931).

The detailed chemical reactions are given and explained in Salle (1948: 325) and will not be discussed here. For our present purposes, it is important that all living cells contain the sulfhydryl group and that not only increase or decrease in cell num-

ber but (in a partial sense) ultimate body size as well, is correlated with the sulfhydryl mechanism elaborated by Hammett and coworkers. Further, sea water does not prevent expression of the reaction and numerous experiments showing similar results were performed on marine invertebrates.

We have here, then, a mechanism within living cells that contributes to cell increase or decrease in number and, at least in the above-mentioned examples, to cell increase in size as well. Opinions on the importance of the sulfhydryl group in cell growth have been more recently re-evaluated (Barron, 1949: 130) and found to be based on "good" evidence. In addition, the probable mechanism has been further clarified. When the –SH group is destroyed by oxidation, the retarding effect on cell growth that results may ultimately stem from enzyme inhibition thus produced (Barron, 1949: 130; Sen and Bhattacharya, 1952: 42). This appears to be the case because some proteins require the presence of the –SH group for enzyme activity (Barron, idem: 108, table 3).

Just how this mechanism might explain instances of dwarfism found in the fossil record puzzled the writer considerably until he read the paper by Harrison (1924: 1009–1022). This author found that "additions of iron of the order of 1/10,000 mg. produces a marked increase on the rate of oxidation of the purified cysteine and glutathione." These compounds belong to the sulfhydryl (–SH) group, and it was the partially oxidized sulfoxide derivative of these groups which Hammett found to have the retarding reaction on cell growth. Minute amounts of iron can cause, as the above experiments show, a marked increase in production of the retarding agent, the sulfoxide from the sulfhydryl. Thus, we have a plausible mechanism for the often referred to dwarfing by iron. Pyrite, an iron sulphide, which characterizes the composition of many "dwarfed" faunas, or if it is oxidized, limonite, might then be related to dwarfing part of a fauna by the above mechanism. The concentration of iron in the beds containing pyritized or limonitic faunas was undoubtedly a very high concentration in terms of the minute amount required to enhance production of the retarding sulfoxide in living cells.

It is also quite possible, as Hammett points out, to retard increase in cell number and yet not affect ultimate body size. In his letter (1951) he states that "dwarf forms may have (the) same . . . number of cells as un-dwarf but (the) cells (are) smaller (Castle). Hence not due to lesser increase in cell number but to lesser constructive substance increase."

The procedure for establishing the dwarfed elements remains unchanged. Finding such diminutive fossils does not establish dwarfism. Growth stages, critical dimensions, etc. are still primary. Once dwarfed elements are shown to be present, the above mechanism may help to explain how dwarfism came about. As a converse of the above mechanism, the presence of unoxidized sulfhydryl might explain giantism in some instances, in species which are also represented in the fossil record by dwarfs. Furthermore, stress should be given to Hammett's observation that the sulfhydryl group may also be a "partial determinant of specific size differences." In his letter, Dr. Hammett elaborates this briefly. Thus he sees it as possibly coming about "through a differential reaction of different cell types to –SH."

Experimentally controlled size variation.— There have been few experiments yielding data on conditions promoting size variation in marine invertebrates. Of these, one of the best is Gajewski's study (1922: 139 ff.) on *Artemia salina*. Schmankewitch had earlier found that several varieties of this brine shrimp occurred in the Odessa salt marshes and attributed the observed variation in morphology and size to differences in salt concentration and temperature. Gajewski collected animals, eggs, salt and slime from two bays near Sevastopol for aquarium cultures. His experiments showed that there was a direct correlation in salt content of sea water and both size and morphologic changes. Animals did not always grow larger in length in water of higher salinity although differences in body proportions seemed always to accompany such changes. Thus, the segment of the post-abdomen that was long and thin at high concentration, became short and wide at lower concentrations. He also found that progeny would show equivalent size variation and morphologic

changes if kept in water of the same salinity as their parents. When new physical-chemical conditions were introduced, the animals lost in the course of two or three generations, what Gajewski calls the "individuality" they had acquired.

Increased salinity up to a point has been generally associated with a tendency to grow larger in marine invertebrates. The Gajewski experiment, however, helps to clarify this generalization. Increased salinity does not necessarily mean a progressive size increase in the greatest body dimension (length, for example). It can express itself in changes of the proportionate length and width of different body segments and morphologic changes of the type of fusion or bifurcation of segments. The latter may or may not contribute to increase or decrease of over-all body size.

The amphipod, *Gammarus chevreuxi*, lives in brackish water ditches in an environment subject to great variation in temperature, salinity, pressure due to depth of water, etc. (Sexton and Wing, 1916: 20). Although the experimenters were primarily interested in the Mendelian inheritance of eye-color in this animal, they found that bacteria retarded growth (cf. Rothschild, 1935: 537–546). In one case a female amphipod took 8 months to become mature and was then only about one-half of the normal size (idem, 1916: 48). How this retardation is accomplished is not clear. The experimenters reported that several kinds of bacteria were present, some fatal, others that retard development but do not injure the animal. One of the latter type makes the water milky. In brief, bacteria-created toxicity introduced into the environment, acted as a growth retardant. Unfortunately, chemical analysis of the water before and after was not undertaken.

Ford (1928: 93–102) carried the above observations further. He experimented with the precise purpose of explaining the mode of inheritance of dwarfing in this animal. He found that dwarfing in *Gammarus* could be of two types, environmental and genetic. Environmental dwarfing could be produced by bacterial infection, feeding dead leaves only with no green food such as lettuce, and in other ways not stated. Genetic dwarfing was found "to depend upon a single recessive factor which has been called "g" (slow growth) as against "G" (normal growth)." *This single recessive reduces growth rate but not size at maturity or final size.* In other words, growth is retarded by the recessive factor for specimens homozygous for it ("gg") but ultimately the so-called genotypic dwarfs grow into normal-sized males and females (idem: 96). At time of extrusion, both "dwarfs" and "normals" are of the same size. During the first 27 days of their development, however, the head length of "dwarfs" increases only 0.04 mm. compared with 0.20 mm. for normal specimens during the same period. "Thus, the difference between the two types increases at first and then diminishes again."

The above findings introduce a factor of importance for paleontologists, namely, differential growth rate for individuals of the same species at precisely the same growth stage. If, in an assemblage of fossils of a given species we find noticeable size variation in specimens of the same general growth stage, differential growth rate may account for it. Had such specimens when in the living state continued to live, such size differences might ultimately have been overcome as in *Gammarus*. This could account for some of the anomalies of size variations reported in the fossil record. Ford's genotypic dwarfs are not true dwarfs. However, if they were found in fossil assemblages, they would most likely be termed true dwarfs.

Seasonal and latitudinal (temperature) variation of size for several developmental stages of the marine copepod, *Calanus finmarchicus*, had been reported by Gran (1902; cf. Marshall, 1933: 111–138). Coker decided to study experimentally the influence of temperature. He used the freshwater copepod, *Cyclops vernalis*. An inverse correlation of size with temperature was found. At the highest temperature the mean length was 1.11 mm., at the lowest temperature, it was 1.62 mm. for females and comparable results were obtained for males (Coker, 1933: 407–435). Other experiments were conducted by the same investigator with the same and different species of copepods on the effect of food deficiency. These showed that the primary effect of such deficiency was "retardation or arrest of de-

velopment or both (extending the period up to six times the normal) rather than mortality or a notable degree of dwarfing." (idem: 430). When, after a prolonged period of semi-starvation, moderate amounts of food were tardily supplied, it was possible that such semi-starved individuals would approximate the maximum size for normal individuals.

Here again, we have the example of retarded development due to some external factor (food deficiency). From the paleontologist's point of view, under such conditions, death and burial of marine invertebrates, living in a semi-starved state, might leave in the fossil record apparent dwarfs. Yet, as Coker and others have found (cf. Mead, 1900: 17-23; Vevers, 1949: 175) overcoming the deficiency, restores normal growth. Experiments on oysters supports this observation (Loosanoff and Engle, 1947; Loosanoff and Tommers, 1948).

Inadequately documented or poorly conceived experiments are reported by Semper (1881) on *Lymnaea stagnalis* and by Loomis (1903: 895). Experiments were performed for which only results but no data are given by Loomis. Small fishes, tadpoles and snails were kept in an aquarium saturated with iron and controls were also set up. Fish and tadpoles had lost from 3.0 mm. to 5.0 mm. in length after eight months in the iron-saturated water. Loomis states that "while the results in the above experiment are not large, they show the dwarfing effect of iron." A loss of length, however, means a decrease in the size of already existing cells, that is, a shrinkage effect as obtained in tanning leather, rather than a dwarfing effect. If Loomis had reported that the animals in the control aquarium were of the same age as those in the experimental aquarium and had at the end of the eight months shown a greater growth, this would indicate a temporary retardation of growth in the experimental animals caused by iron in solution. In that case it would not demonstrate dwarfism unless, after normal conditions were restored to the experimental group, they failed to grow normally. The Loomis experiment does not, then, show the dwarfing effect of iron.

Iron and other metallic cations as factors influencing size variation.—Cooper (1947–48: 279–313; cf. Cooper, 1933; Atkins, 1928) has classified the forms of iron in sea water into two major groupings: uniformly dispersed iron and aggregated or particulate iron. Ferric hydroxide or phosphate that flocculates or is excreted at middle depths appears to have the following career (Cooper, 1947: 287). It can either be caught by filter-feeding zooplankton, be adsorbed upon phytoplankton (diatoms) (Harvey, 1937–38: 205–219) or slowly settle to the bottom. Once on the bottom, turbulence, caused in several different ways (tides, currents, etc.), help to circulate these particles. Iron-containing feces extruded by sessile and free-swimming animals, adds to the amount of particulate iron on and near the bottom. Subsequent breakdown of particulate iron is achieved in two ways: dissolved by acid digestive juices in intestines of filter feeders and breakdown by bacterial intervention of particulate iron incorporated in waste products. Both modes of breakdown of particulate iron have the end result of dispersing iron in solution or as even finer particles. In other words, there is a complex mechanism involving intervention of various organisms which are most abundant for transforming ultimately large quantities of particulate iron in sea water into ionic iron, colloidal organic or inorganic compounds. While the existence of this mechanism is implied in the important paper by Cooper (op. cit.), its applicability to the problem of the role of iron as an influence on size variation among marine invertebrates seems to have gone unrecognized.

Sherwood (cited in Cooper, op. cit.: 287) performed the following experiment. A litre-measuring cylinder about 0.4 m. high was filled with estuarine water. On the bottom of the cylinder, the investigator placed a single mussel. It was then covered by a thick suspension of red oxide (Fe_2O_3). Results were as follows: at lapse of one hour, the mussel had cleared much of the suspension from the water; at lapse of two hours, "no trace of the opacity could be seen." Cooper concludes from this experiment that "given a certain amount of tidal mixing, a bed of mussels should have no difficulty in the course of a few days in clarifying a bottom layer of water 5–10 m. thick." If the argument is raised that mussels do not

live at a depth of 90 meters, Cooper (op. cit.) points out that *Pinna*, a large mollusc with similar feeding habits, does live at such depths.

A most penetrating and valuable observation follows from the above. Given a water column with considerable particulate iron in suspension and over a period of time, molluscs of the type of *Pinna* would deplete this column of iron, "converting it first into feces and much pseudo-feces which would tend to accumulate in bottom deposits, only slowly returning to the water." The surface flora (phytoplankton), if the iron was not replenished, might be adversely affected by the shortage thus created. "Thus, in certain hydrological circumstances, an inverse relationship may develop between a dense bottom molluscan fauna and the phytoplankton production many meters above." (idem: 288). We have here a mechanism which when linked to the food chain prevailing in the sea, might adversely affect the food supply in any given area in which it was operative. Upset of the "balance" at one point could have a chain effect on animal life in the area of phytoplankton depletion. This probably happened many times in the geologic past. It has particular relevance to pyritic and limonitic "dwarfed" or "depauperate" faunas. Depauperization might then be attributed in some instances to an upset in the normal food chain due to the above-described mechanism. Molluscs are particularly common in such faunas, a fact which appears to strengthen this line of reasoning.

A further point to emphasize is the fact that in an area with iron-rich waters, retardation of cell increase might be a factor of importance. This might be due to the role of iron facilitating the production within animal cells of the retarding agent, sulfoxide. The large number of pyritized and limonitic fossils of "normal" size makes it clear that none of these factors are universally or always effective. An Australian pyritized fauna of Tertiary age, recently mentioned in connection with a study of supergene iron sulphides (Edward and Baker, 1951) for example, was found to be a normal fauna and not dwarfed or depauperate (Teichert, personal communication, 1951). Instances of this type are not infrequent. Pyritized ammonoids in the S.U.I. Museum collections from horizons of various geologic age, are often as large or larger than normal.

Zo Bell and Feltham (1934: 169–176), using a medium of diluted sewage, found that "in general, concentrations of iron up to 4.0 millimols ferric iron or 2.0 millimols ferrous iron did not inhibit the multiplication of sewage bacteria. In fact, small quantities of iron stimulated bacterial growth. It made little difference whether the chloride, sulphate, citrate or acetate of iron was used provided the H-ion concentration was properly adjusted." Lead and bismuth salts, however, were found to retard colony development and inhibit growth. Such was also the case for higher concentrations of iron. An earlier experimenter, Lieske (cited in Harder, 1919: 77) found that *Spirophyllum ferrugineum* will not grow in media in which ferrous bicarbonate is not present and that other iron salts cannot substitute for the bicarbonate. When the metallic cations, Mn, Zn, W, Cu, etc. were substituted for the iron cation, no growth took place.

Toxic effects of certain metallic cations (Cu, Pb, Sn, Hg, Ag) leading to the death of organisms, were called "*oligodynamik*" by Nägeli (1893; see also Dethier, 1950, Marks, 1938, Prytherch, 1931, Warren, et al. 1949, 1952, Bowen, 1940). Other investigators have also found that particular cations retard or stop growth. Professor Witschi (personal communication, 1952) found that using copper pipe perforated to allow water to trickle out at several points, seriously retarded growth of frog larvae and algae. Use of iron pipe eliminated this condition. Locke (1895) also found metallic copper noxious to certain animals. Weiss 1948: 116–119) found that barnacles exposed to copper and zinc exhibit malformations probably due to interference with calcium metabolism.

For crustaceans, arachnids, and molluscs, copper in the form of haemocyanin performs a respiratory function. The "liver" in most marine invertebrates appears to be particularly rich in copper and other metallic cations (Webb, 1937: 528). One might suspect that for marine invertebrates such as crustaceans with a high copper content

held in organic combination, they would resist the toxic effects of copper ions more than non-copper storers. This is not the case. Löhner (in Webb and Fearon, 1937: 491) found copper storers to be just as susceptible to toxic effects of copper ions as marine invertebrates that do not contain haemocyanin. It has been observed that crustaceans such as the crayfish and ostracod are not susceptible to the toxic or "oligodynamik" effect of Cu (Scott, 1948: 67). In this case we cannot attribute such resistivity to the presence of haemocyanin. On the other hand, there is some experimental evidence to show that some crustaceans are susceptible to toxic effects of Cu. Hunter (1949: 8–124) experimented with the amphipod, *Marinogammarus marinus*. He found that for this species, in artificial sea water, concentrations of Cu below 50 mg./l. were virtually non-toxic while concentrations above this were. For distilled water, however, low concentrations of Cu (0.5 mg./l.) proved toxic. Copper appeared to depress the rate of oxygen consumption and the experimenter attributed its toxicity to interference with either the respiratory or osmo-regulatory system or both. Hunter (idem: 123) put forth an interesting hypothesis to account for the action of heavy metals on complex animals. Given a series of concentrations from A to E where A is the lowest concentration of the metallic cation and E the highest, the following effects noted by different investigators may form an "overlapping series":

Concentration

A—stimulatory effect
B—inactivation of an enzyme system
C—interference with respiration by decreasing the blood pigment's transport efficiency (cf. Erichsen-Jones, 1942: 161) or, interference with excretion or nervous coordination
D—coagulation of mucus or other essential secretions
E—coagulation of protoplasm or fixation occurs

While little consideration has been given to the effects of such toxicity on growth of marine invertebrates, the effect at Concentration B seems to be important in this connection. Elvehjem (1935: 300) reviewed the literature on the subject that in general indicates "the interaction of copper and sulphydryl compounds may play an important role in the activity of certain enzyme systems." Thus, copper salts are known to have a catalytic effect on the oxidation of cysteine (-SH group) and oxidation of SH-glutathione is reported to be accelerated similarly (idem: 500; cf. Erichsen-Jones, op. cit.: 153). Chalkley and Voegtlin (1932: 535–560) for example, found that where Cu salts inhibited mitosis in *Amoeba proteus*, glutathione restored it. Inhibition in this case may be attributed to the oxidation of the –SH group while addition of glutathione would negate this effect. This places copper in the same role as iron. It will be recalled that Hammett and coworkers found the partially oxidized sulfoxide to have a retardative effect on cell growth in number. Thus, we may have here an approach to the explanation of growth retardation associated with *oligodynamik* waters. It will be obvious by reference to Hunter's scale of concentrations given above, that the very toxicity that can lead at lower concentrations to retardation of growth, can, at higher concentrations create conditions prohibitive for life itself.

Iron cations are also efficacious in annulling the toxic effect of *oligodynamik* water. Cramer (cited in Locke, idem) found ferric hydrate and Locke found ferric oxides as well as other substances (graphite and tricalcic phosphate) had this effect.

For particular organisms then, there is a minimum and a maximum tolerance of the metallic cation, iron. Within such limits growth may be promoted; beyond these limits, a toxic effect may result. For other metallic cations, Pb, Cu, for particular organisms, there may be no minimum non-toxic quantity. Enrichment of *oligodynamik* water by iron or calcium phosphate, however, should restore normalcy in the environment and in the growth of certain organisms living in it.

Uspenski (1927: 1–93) found that "the optimum concentration of inorganic iron for individual algae lies between 0.2 and 2.0 mg. Fe_2O_3 per liter. Iron concentrations which exceed the optimum two or three times are strongly toxic." He found for *Microspora amoena* that at slightly more than 1.0 mg.

Fe_2O_3 in a liter of water the filaments were short and showed iron deposition. At 1.5 mg. the algae disappeared entirely or showed only slight development. These effects may be taken as expressions of growth retardation in toxic concentrations of iron oxide. Uspenski noted also that greater or lesser sensitivity of algae towards iron depended upon the chemistry of its cells and that an acid cytoplasm is very resistant towards iron. Retardation of increase in cell number due to partial oxidation of sulfhydryl in the cells may be a factor in this case. Hopkins (1934: 209–239) considered the problem of iron-ion concentration in relation to growth and other biological processes. He found from experiments with *Chlorella* cultures that "iron is effective physiologically in the form of its ions. The total soluble iron may vary within wide limits and still have the same effect, either on growth or toxicity, providing the iron-ion concentration is the same." Iron in solution and not particulate iron is physiologically effective in growth. Hopkins found that inhibition of growth in *Chlorella* occurred as the OH-ion concentration or as the citrate content increased. In both cases he attributed this effect to depression of the ferric ion concentration. Uspenski had earlier observed that "organic matter paralyzes the effect of iron" on growth by buffer action (*Pufferwirkung*) (op. cit.: 3). Hopkins summarized this point by noting that "large amounts of iron which in certain cases would be very toxic, in the presence of organic matter may be entirely harmless" (idem: 209).

The above observations based on experiments shed new light on many problems that beset the paleontologist dealing with pyritized or limonitic faunas. Why, for example, is presence of a large amount of iron, as evidenced by pyritized faunas, not necessarily influential in size variation of marine invertebrates? Buffer action of organic matter could render a potentially toxic iron concentration physiologically harmless. Thus, in cases of normal-sized pyritized faunas, contrasted with dwarfed or depauperate faunas of the same composition, buffer action in the former and its absence in the latter could account for the results. Then again, it is not the total iron in sea water, but only the ionic form (iron in solution) that is physiologically active. According to Cooper (op. cit.: 300), ionic iron (uniformly dispersed iron), consists of the following cations: Fe^{++}, $FeOH^{++}$, Fe^{+++}. In true solution in sea water at equilibrium these will not exceed more than 10^{-8} mg. atom m^3. Also present in true solution is ferrite iron, H_2FeO_3'. These, then are the physiologically effective forms of iron. Particulate iron can be brought to the ionic form in the acidic environment of the intestines of organisms as already discussed earlier.

Cases of experimental giantism in rats are on record. It is suggested that after injection of the growth hormone, some substance, *perhaps* iron, becomes more abundant in the epiphyses and the periosteum thereby accelerating bone formation (Futcher, 1933: 42, 71). It is curious that a factor generally accredited in geology as being a dwarfing agent, among marine invertebrates, may lead to *giant* individuals in rats and can definitely promote, in small quantities only, growth of sewage bacteria, algae, and diatoms (Harvey, 1933: 268).

Sarasin (1917: 207–208) reported finding in "Lac en 8" in New Caledonia, a stunted (*verkümmert*) living fauna consisting of tiny crustaceans, worms and fish. The largest fish, *Galaxias neocaledonicus* was 76 mm. long. The lake is environed by dwarfish (*zwerghaft*) and deformed (*verkrüppelte*) vegetation. The author attributed the stunted fauna and vegetation to the dwarfing effect of iron (*die eiserne Not*). While this was an incidental observation, it is noteworthy as one of the rare reports of living forms in the natural state allegedly dwarfed by iron. Study of an Army map of New Caledonia (Reprint October, 1942, Sheet 7) indicates that even though Sarasin found no inflow into this lake it is at the head of the River des Lacs and is probably fed by rainwater and underground springs. At times, minor streams apparently ensue from the lake from the northwest and south sides, probably after heavy downpours. All of this suggests that water does circulate in this lake from time to time. The lake is about 230 m. above sea level. If this fauna is truly dwarfed or stunted, it may be accounted for in several different ways. The low proportion of trihydrol and high proportion of monohydrol might contribute to the

retardation of growth. Negligible buffer action by organic matter or intervention of organisms on bottom muds containing iron-rich feces might favor a higher concentration of ionic iron. Such ionic iron might then exercise a retarding effect on increase of cell number and ultimately on over-all body size.

Salinity, pH, and other factors affecting size variation.—Salinity: Although it has been generally reported that there appears to be a direct correlation between size and salinity (Gunter, 1945: 55–56; 1947: 77–79) and that in saltier water invertebrates tend to be of larger size, there are but a limited number of studies of such correlations. It has been established that ionic regulation is a universal phenomenon among marine invertebrates although the extent of regulation differs from group to group.

Ionic regulation may be defined as maintenance in a body fluid of concentrations of ions differing from those of a passive equilibrium with the external medium (Robertson, 1949: 182). It has been shown (idem: 182–200) that such regulation expressed itself as an accumulation of the potassium and calcium ions and a small diminution of SO_4. This appears to hold for coelenterates, echinoderms, polychaete worms, lamellibranchs and gastropods. In these groups Na and Cl are essentially in equilibrium across boundary walls. Elimination of Mg is slight. Regulation may be pronounced as in the case of the decapod crustaceans and the cephalopods. The former excrete excess Mg and SO_4, while the latter eliminate Na and SO_4 hence lowering the sea water equilibrium values in their plasma. In the case of crustaceans and cephalopods, regulation of the composition of the blood seems to be under partial control of the excretory organs. For coelenterates and echinoderms regulation may be confined to the bounding layer of cells as in *Aurelia*, or the gills may play a role as in *Echinus*.

Any explanation of the reported influence of increased salinity on growth of marine invertebrates must take into account the ionic regulatory system which differs in different organisms. Conceivably malfunction of the system in any marine invertebrate can have pathological effects among which size variation may be included. Nevertheless, a specific rather than a generalized approach seems necessary. Thus, variation in the *degree* and *kind* of ionic regulation characteristic of a given marine invertebrate can explain certain anomalies in the paleontological record. An excess of Mg ions, for example, would be more likely to have pathological effects on certain pelecypods and gastropods than on cephalopods. Thus, a fossil assemblage could readily contain forms that had been adversely affected by a particular high concentration of a certain ion in association with others apparently unaffected in terms of size variation.

The relative toxicity of various anions (Cl, Br, I, SO_4, SCN, NO_4, PO_4, etc.) have been studied by many investigators. Erichsen-Jones (1942: 170–181) reviewed the earlier work and performed experiments of a similar type on the planarian, *Polycelis nigra*. It was found that for the most part, anions are "decidedly less toxic" than cations. The most toxic anion (OH) was much less potent in its effect on the test animal than Cd, Cu, Au, Ag and Hg. Mercury, for example, was found to be 40 times as toxic as OH. Some appreciation of the toxicity of different anions can be gleaned from the interpretation that sulphides and cyanides inhibit protoplasmic oxidation (Mitchell in Erichsen-Jones, idem: 176). Strong alkalis have been generally reported to dissolve proteins and bring about the rapid necrosis and destruction of animal tissues. The effect of sodium hydroxide solutions on *Polycelis nigra* strikingly confirms such reports (idem: 176–177). In terms of the present discussion, these findings indicate that if any influence is exerted on size variation of marine invertebrates, one can expect such influence to be greater due to effective concentrations of metallic cations than to equivalent concentrations of the various anions.

Milne (1940: 69–87), in a study of estuarine ecology, found that "generally the organisms become less numerous and smaller towards the lower end of their salinity range, as very obviously shown without measurement by *Laminaria* and *Mytilus*." The author found the main limiting factor to be "salinity" and noted that "average

salinity decreases and range and rate of fluctuation (in size) increases in the up-river direction."

Worley (1929–31: 233–240) reported on the correlation between salinity, size, and abundance of intertidal barnacles found in the Puget Sound region. Only adult barnacles were studied. It is well known that the shape and form of barnacles is the result of crowding (Moore, 1935–36b: 279–307). In Worley's correlation, this factor was taken into account. He found that different species of *Balanus* reacted differently to less crowding and higher salinity. *Balanus glandula*, showed an increase and *Balanus cariosis* showed a decrease in maximum size under these conditions.

An increase or decrease in salinity may be correlated with size variations. Such correlation may be part of a complex of factors each one of which would also show a correlation. Thus, Humphrey and Macy (1929: 205–208) studied the factors controlling the size of two species of the tidal pool snail, *Littorina*. They found that "the average volumes . . . increase with the rise in salinity, oxygen content, temperature, and elevation above high tide, and decrease with a rise in acidity." Some of these factors are, no doubt, functions of one another.

McClendon (1916: 135–152) for example, showed that there was an important relationship between the physiological action of the sodium, potassium and hydronium ions and the hydrogen ion concentration. Experiments with the lagoon jellyfish, *Cassiopeia xamuchana*, showed that pure solutions of $MgCl_2$ and $CaCl_2$ paralyzed the animal. Additions of KCl or NaCl restored pulsation. The restorative effect of the sodium ion was found to be inhibited by an increase in the hydrogen ion concentration. The experimenter concluded that the above-named ions increased permeability of the plasma membrane while the calcium, magnesium and hydrogen ions inhibit their action "thus causing decrease in permeability when the antagonist ions are present." This may explain the results Humphrey and Macy obtained and may also have bearing on the reported efficacy of increased salinity as pertains to larger size in marine invertebrates.

Pereira (1924: 1294–1296) found that "in general, the more acid the medium the less is the oxygen consumption per gram of fish per litre of water per hour." Thus, increased acidity not only inhibits the action of certain ions but directly affects the rate of oxygen consumption. Similar findings have been reported by McClendon (1917) and Powers (1920). Other experiments on marine invertebrates indicate that certain substances like KCN decrease the rate of oxygen consumption (Hyman: 1919–1920). Humphrey and Macy noted that size increased with rise in oxygen content while it decreased with rise in acidity. The latter result may be due to a depression of the rate of oxygen consumption by the hydrogen ion.

Davis (1940) studied the ecology and geologic role of mangroves in Florida. Of particular interest for the present discussion are the dwarf form of mangrove communites he described. These were found on salt flats, in brackish water and in fresh water. The facies on the salt flats where water is infrequently changed by the tides or currents during some periods become very salty. The author attributes dwarfism in this instance to both the extreme salinity and poor aeration of surface waters. The brackish water facies occurs in an environment of 1.556 per cent salinity and in stagnant water. The author merely states that conditions for mangrove growth are unfavorable. The fresh water facies occurs in an environment with average salinity of 0.008 per cent. Dwarfism of this latter facies is not considered to be related to salinity. Based on our earlier discussion, decrease of permeability and low oxygenation appear to have been factors affecting growth in the salt flats and brackish water respectively. The polymeric composition of water may have been involved in the dwarfing of the fresh water facies along with other factors. The "rather poor" fauna of mangrove swamps consists of three elements: the element of the swamp proper, the hypohaline element, and the element found on the rocks (Oyama, 1950: 4, 7). The hypohaline molluscs live in a zone equivalent to Davis' fresh water facies. Data on size variations for molluscs transgressing the different zones or of the hypohaline element compared to the inhabitants of saltier waters

are not available. The forms Oyama described included the swamp element proper and the rock element. Both distinctly large-to-very large species of *Telescopium* and of *Geloina* occur. Small species of *Littorinopsis*, etc. are also present.

Low salinity was one of the factors thought to contribute to the dwarf form of the Dingle anemone (Rawlinson: 1933–34: 901–919). The river water in which this form was found attached to mooring chains or rocks is brackish and fouled by abundance of silt, presence of an oil jetty, and sewer seepage. Down river, in somewhat higher salinity, undwarfed colonies occur.

Thus, studies of the flora or fauna of the coastal marine, estuarine, river, intertidal, and coastal marsh environments all indicate that high or low salinity is a factor in size variation.

pH.—Variation in pH has, as already noted, an important influence in oxygen consumption in some invertebrates. McClendon (1916: 148) observed that the presence of animals or eggs causes a rapid change in the pH of sea water. Death of all animals occurs within certain pH limits. Various substances present in sea water act as buffers that tend to prevent any big change in the pH of sea water: bicarbonate, minute traces of phosphates, silicates, borates, and organic matter. That is why relatively large additions of alkalis or acids are necessary to change the pH (Harvey, 1928: 75–76). The animals needing to tolerate the greatest and most rapid changes in both pH and O_2 appear to be those living in burrows among the *Ulva* at low tide level (Powers, 1920: 382). In contrast, plankton of the open sea have to tolerate relatively small differences in hydrogen ion concentration and hence pH "does not play any well marked part in regulating the fauna" (Harvey, idem: 80; Powers, idem).

Fisher (op. cit., cf. Scott, 1948: 65–70) observed of the Ludlowville that both size and quantity of individuals will be considerably reduced should the pH decrease. That is, there would be an increase in hydrogen ion concentration and hence greater acidity. Only one study known to the writer directly relates decrease in pH with size of individuals—the study of Humphrey and Macy previously discussed. In that study pH is related to a complex of factors and it is far from conclusive that pH alone could exercise a control on ultimate body size. Furthermore, rapid changes in pH are not to be anticipated in the presence of buffers among which organic matter plays a role (Pauling, op. cit., 389–391). In a fouled environment where H_2S is being generated, a considerable amount of organic matter will be in the bottom mud and overlying water. That quantity may be sufficient to buffer any rapid change in pH. Hence, it is uncertain on both grounds that mere decrease in pH can directly influence size and quantity of individuals.

Other factors.—There has been a tendency to attribute size variation to a single or, at best, a few alternative factors. However, examples are known where size variation may definitely be attributed to crowding as in studies of *Balanus* (Moore, 1935–36b, 36c) and molluscs (Ford, 1925: 531–558). Bacterial infection as earlier noted, can produce dwarfs or giants in certain forms. A tendency to gigantism in the gastropods, *Purpura lapillus*, variety *imbricata* from a sub-littoral habitat was observed (Moore, 1936–37a: 85) and attributed to absence "of the factor which normally inhibits growth at maturity." Curious size variations accompanied by morphologic differences have been noted among tadpoles of the same age raised in the same tank (Witschi, 1936: 611–651) where shape of tank or number of collisions among animals may be a factor. Size variations among eggs and larvae of *Echinus esculentus*, *Ophelia bicornis*, *Sabellaria alveolata* have been reported (Wilson, 1951: 1–18; plate 1). Normal plutei of the latter species were obtained from the Celtic Seas while unhealthy (stunted) plutei of the same age and same species were found in sea water from the English Channel in the region of Eddystone. The author suggests that the unhealthy plutei may be accounted for by a deficiency disease.

Study of the biology of *Echinus esculentus* (Moore, 1935–36a: 109–123) whose shells show annual concentric rings which served as a basis for estimating growth rates on different grounds, revealed a variation in size attained by different year groups. These differences were attributed to a complex of

factors which included: food supply for year in question, variation in time of hatching and hence in time available for growth before the onset of winter, and variation in monthly mean temperature. Similar variation in growth rate on different grounds is reported for *Littorina littorea* (Moore, 1936–37b: 721–742). The latter, based on the data given, appears to be related to the available frond space provided by fucoid growth which acts as a substrate for these animals. Thus, growth rate is less on the grounds where fucoid growth is less.

Factors of this type would hardly be decipherable from the rock record in the case of fossils of the same species showing marked size variation. It is true that in the geologic past, as at present, anomalous factors of this type were most likely the exception or relatively infrequent. Nevertheless, in any given study of the fossil record as pertains to observed size variation within a given species, one should be cognizant of such factors which might apply in specific instances. Prior to any other explanation, it is desirable to establish that difference in size of specimens of the same species does not "imply the presence of younger stages" (Teng, 1951: 672).

Size variation within a species geographic range.—Moore (1936–37a: 61–69) provides data on size variation within part of the broad geographic range of the common carnivorous gastropod, *Purpura lapillus* Linn. This is shown in Table 11.

Table 11 indicates that there appears to be a definite decrease in size towards the southern limit of the range while towards the more northerly part there appears a decrease also, which is relatively slight. In terms of the fossil record, a distribution of this kind might lead to the interpretation that more than one species was represented or that the smallest specimens (latitude 40°) had their growth impaired by intervention of some external factor. If the smaller specimens were pyritized while the others were not, this interpretation would be even more acceptable. Yet, these and equivalent interpretations would be incorrect since normal size variation within a species geographic range is involved.

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TABLE 11.—SIZE VARIATION OF *Purpura lapillus* LINN. FOR THE PORTION OF ITS GEOGRAPHIC RANGE ON THE EAST SIDE OF THE ATLANTIC*

Latitude (degrees) (North)	General Locality (Name)	Mean Value Max. Height (mm.)	Frequency	Number of Localities
42	Coast south of Cape Finisterre	26	s[1]	6
42–60	Cape Finisterre North, to just south of Bergen	35	a	95
above 60	Bergen and northward	32	s	14

* Data from Moore (1936–37a: 61–69).
[1] s—sporadic; a—abundant.

ADDENDUM

Since this paper was completed and while it was awaiting publication, additional material of particular relevance to the discussion has either just been published, or has just come to the writer's attention.

The tendency for planktonic animals to grow to larger size in cold water than do similar animals in warm water is given much support by numerous investigators who have made direct observations on living populations found in various waters (cf. Sverdrup, et al., 1946: 855–857). In addition to the reasons already proposed to explain this phenomena, it is suggested that increased density and viscosity of cold water may be still another since these properties enable large forms to keep afloat more successfully in cold water than in warm water (idem: 857).

Anomalous occurrences which apparently contradict Wimpenny's "central tendency" (i.e., larger size at higher latitudes) have already been noted. Evidence to accommodate some of the anomalies to the trihydrol hypothesis is offered in several valuable studies cited by Sverdrup, et al.: Jesperson (1939) on size stratification in *Calanus finmarchicus* in Greenland waters; Koford's study (1930) of 1,000 individuals of a single species, *Tintinnus tenue*, where those taken at stations with surface temperatures of 19°–23°C. were predominantly larger than those from stations with temperatures of 24°–28°C.; the bathymetric size distribution in the Radiolaria belonging to the Challengeridae where size increases with depth.

Even more impressive are the data provided by Steuer (1933) for three varieties of the copepod *Pleuromamma gracilis* taken in the Benguela stream. In the uppermost warmest waters (upper 400 meters) he found a dwarf race ("*Zwergrasse*"), variety, *minima;* size, 1.68–1.79 mm.; below 500 meters, in the coldest water layer, he found a giant race ("*Reisenrasse*"), variety, *maxima;* size, 2.11–2.15 mm., while in between these two layers, he found a medium-sized race ("*Mittelrasse*"), variety, *piseki;* size, 1.83–1.96 mm. Thus, dwarfed and giant varieties of the same species are, in this instance, directly correlated with temperature depth zones. Further observations by Steuer indicate that copepod response to cold or warm waters is extremely sensitive. *Acartia negligens* and *A. danae*, for example, become smaller in transition from the Canary current to the warm Guinea stream. However, *A. danae* is larger in the south Equatorial current which is mixed with the cold water of the Benguela current.

It is altogether possible that the trihydrol hypothesis (i.e., the physiological effects of previously frozen water) may explain these size distributions. A recent discussion devoted to arctic waters (Dunbar, 1952: 61–67) takes this hypothesis into account.

Ingle (1950: 338–339), reporting on summer growth of the American oyster, *Ostrea virginica*, observed that growth in Florida waters was both considerably more rapid and more extended than in northern waters. Thus, a length of one inch is achieved in Florida in 5 weeks whereas this is nearly a year's growth in northern waters. A length of 4 inches attained in Florida waters in 31 weeks would require approximately 208 weeks in northern waters. This finding has a double interest: (1) it goes counter to Wimpenny's "central tendency" and may fit the type of explanation described above, (2) it indicates that certain fossil pelecypods, for example, may be of the same size at different localities and yet ontogenetically be of different ages due to the factor of latitudinal distribution.

Chronic (1952: 110) rejects the interpretation that the reduced size of gastropods and pelecypods of the Kaibab can be explained by dwarfing due to low salinity. This is of interest, since her evidence was not primarily assembled to substantiate this conclusion. She finds the fauna to consist of (a) an abundance of small undwarfed forms adapted to some special mode of life, (b) a high frequency of juveniles. The special mode of life is suggested to have been dense growth of seaweed upon which small molluscs lived. This finding is in accord with the general thesis of the present paper. Fuchs (op. cit.), Termier (1952) and Dr. Haas (oral communication) have all indicated that such small assemblages associated with *les herbiers* or an *Algenwald* lived primarily in "nurseries"—hence the high frequency of juveniles among these fossils. Larger (adult) forms were effectively sieved out or kept out of the area by the dense

vegetation. Chronic points out that in the Kaibab "there is no positive evidence of the existence sea weeds." If they were there one would expect a relatively high organic content in the fossil sediments. On this point no information is given. Instead, she relies on the dual nature of the fauna, i.e., thick-and-thin-shelled types. She reasons that while the latter clung to seaweeds, the former were mud-burrowers or crawlers on the bottoms of the seaweed forest. Even though Chronic indicates that there is no evidence of sorting, might not an alternative explanation be selective bottom sorting? The evidence for this is the generally small size of the molluscan fauna. It should be noted that she also reported beds composed predominantly of one species, for example, *Schizodus texanus*. These occurrences were attributed to reduced salinity. Might not these be coquinas or coquinoids caused by storm-generated wave action? If so, this would exclude salinity as a cause. At ann rate, dwarfism as a factor in size distributioy in the Kaibab may be definitely ruled out.

Ross (1951: 26) speaks of the "apparent small size of the fauna" (trilobites of the Garden City formation) and notes that a restricted environment in the Logan area and a dwarfed fauna have been postulated. Further, he indicates that he is not fully in accord with this view. Earlier discussion in the present paper on so-called dwarfed trilobites casts serious doubt that dwarfing can be demonstrated in any trilobite fauna.

Brill (1952: 809–880) refers to dwarfed pelecypods (*Allorisma* sp.) up to 5.0 mm. in length occurring in a limestone bed of the upper Yeso (Leonardian) west of Rowe, New Mexico. Conceivably, these are true dwarfs. However, reference to mere smallness in size cannot establish that fact.

Among deep-sea Antarctic hyaline Foraminifera several dwarfed species are reported (Kierstead and Robinson, 1952). However, measurements, etc. are lacking in the report, thus making evaluation difficult.

In this connection, Myers' (1943: 439–457) work on *Elphidium crispum* is of interest. Although unusual, samples of a population of this species were obtained in one region that as a result of winter turbulence had been sorted according to size. Myers found that the rate of growth is 40% greater and the diameter of the test 60% larger in the sublittoral zone than in the littoral zone. The difference in growth rate and test size was attributed to relative abundance of food available. It was further observed, that in tropical regions, where growth rate is somewhat less but more continuous, the tests are thicker (i.e., growth has been retarded) than those produced at higher latitudes. Another aspect of Myers' report relates to dense growing semi-rigid fronds of coralline algae of tide pools. In a 1 cc. sample, he found 573 living Foraminifera including 91 *E. crispum* and 474 animal associates including Mollusca, Annelida, Arthropoda, Bryozoa, and Nematoda. These animal associates were either minute species or juvenile stages of larger species.

Beebe (1928: 71) reported an interesting example of the occurrence of thriving juvenile tarpons in land-locked sulfurous lagoons in Haiti. It would be impossible for any adult to enter the Haitian lagoon to deposit its eggs because of the shallowness and muddiness of the lagoon. Presumably the eggs are scattered in the gulf, sink to the bottom, and hatch. The young then migrate either as leptocephalids or as very small larval fish into the lagoon before the season when it becomes cut off from the gulf. Here, then, is an instance among marine vertebrates where depth of water effectively sieves out adult forms. The mechanism from deposition of eggs to larval migration into the lagoon may have parallels among marine invertebrates.

A recent paper (Termier, op. cit.) reviews, in some detail, the significance of grass-meadows and pyritic faunas (Ord.-Cret.) Among the observations made are: (1) the goniatites of pyritic faunas represent not dwarfed, but young forms, (2) the richness of pyritic faunas in goniatite juveniles would be explicable by high infant mortality, (3) the majority of pyritic faunas are formed in grass meadows.

The first two of these observations conform to those independently reached in the present study based on measurements and study of growth stages. The third observation requires some qualification where no evidence of a grass-meadow occurs in the fossil sediments.

Since catastrophic death has been postulated for the "Dry shale fauna," it is of interest to add that given relatively constant conditions such as exist in the shallow waters of the Gulf of Mexico, "over (a period of) a million years such mass mortalities may occur between 100,000 and 200,000 times" (Gunter, 1947: 675). This can help to explain why the limonitic fauna found in the "Dry shale" also occurred in the shale member of the underlying Dover limestone. Constancy of conditions leading to a recurrence of mass mortality seems indicated.

Regarding the function of the —SH group in enzyme activity, Vallee (1951: 368–376) reiterates that (a) about 50% of all known enzymes require free sulfhydryl groups for activity (b) metal ions can react with such sulfhydryl groups thereby *inhibiting* these enzymes. Thus, most recent work appears to substantiate the premises behind the explanation for the growth-retarding effects of iron-bearing and *oligodynamik* waters given in the present study.

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NAUTILOIDS AND AMMONOIDS OF THE PENNSYLVANIAN "DRY SHALE FAUNA"

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ABSTRACT—Four species (unnamed) of nautiloids and seven species (two unnamed) of ammonoids are recognized in the Upper Pennsylvanian "Dry shale fauna" of Kansas.

INTRODUCTION

THE limonitic "Dry shale fauna" ranges through the upper Dover shale member, the lower and upper Dry shale, and probably the Grandhaven shale in the Upper Pennsylvanian of Kansas. This fauna is described and figured in this issue of the JOURNAL. The two previously recognized species of ammonoids, *Imitoceras grahamense* and *Goniloboceras goniolobum*, found in the fauna are adequately described in the literature (Miller and Downs, 1950; Elias, 1938). However, the nautiloids and gastrioceratids have not been previously studied. It is the purpose of the present paper to fill this gap.

Elias (1933: 691–700) refers to two species, "*Gastrioceras* (probably the young of G. excelsum)" and *G. welleri*. The former presumably came from the Dry shale of the Emporia region, the latter from the same formation (or Dover shale?) in the region of Piedmont, Kansas. These two species have recently been placed in the synonymy of *Eoasianites* (Miller and Furnish, in press). Thus, the gastrioceratids described here, which differ from both of the above species, are the only ones presently known from this fauna.

It may be observed that extensive collections by the author provided an extremely sparse yield of poorly preserved nautiloids or gastrioceratids, whereas at the same localities *Imitoceras grahamense* and *Goniloboceras goniolobum* were abundant. Fragments of nautiloids of all species represented fall within pebble size grades. Since the major grade for the rest of the fauna was found to fall within this size, the relative sparsity of nautiloids cannot be attributed to exclusion by selective sorting.

Based on all the information presently available, the nautiloids and ammonoids of the "Dry shale fauna" now include:

	Locality	
Nautiloids	Emporia	Piedmont
Metacoceras sp. 1	X	—
Metacoceras sp. 2	—	X
Mooreoceras sp.	—	X
Pseudorthoceras sp.	—	X
Ammonoids		
Goniloboceras goniolobum	X	X
Imitoceras grahamense	X	X
Imitoceras grahamense?	X	—
Eoasianites sp. 1	—	X
Eoasianites sp. 2	—	X
Eoasianites welleri	—	X
Eoasianites excelsus	X	—

Based upon the criterion of suture spacing, all nautiloid and ammonoid specimens discussed in this paper represent juvenile growth stages. This bears out the conclusion reached from a study of the other elements of the "Dry shale fauna" (Tasch, this issue), namely, that the fauna has a generally juvenile character.

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LOCALITIES

(Lyon County): *Dry E-1.*—Sec. 10, T. 19 S., R. 11 E. *Dry E-1a.*—Park South of Emporia Golf Course, Emporia, Kansas. (Greenwood County): *Dover P-1.*—SW/cor. SE¼ SW¼ SW¼ sec. 5, T. 28 S., R. 10 E., cornfield right side Hwy. K-96 going West, 1½ miles NE of Piedmont, Kansas. *Dover P-2.*—330 ft. West of Dover P-1, left side of Hwy. *Dover P-3.*—WL/NW¼ NW¼ NW¼

sec. 8, T. 28 S., R. 10 E., road ditches on both sides going South from Hwy. K-96.

SYSTEMATIC PALEONTOLOGY

Genus PSEUDORTHOCERAS Girty, 1911

PSEUDORTHOCERAS? sp. undet. 1

Plate 50, figures 13, 14

The only characters discernible in the crushed fragment of a limonitic internal mold are the apparently central siphuncle, the circular cross section, and the concentric weathering of the mold. Based on the first two characters, the specimen is tentatively assigned to the genus *Pseudorthoceras* (cf. Miller, Dunbar and Condra, 1933: 77–81; Miller and Youngquist, 1949: 18).

Remarks.—*Mooreoceras* and *Pseudorthoceras* are reported commonly to occur in association in the late Paleozoic (Miller and Youngquist, idem). This is of interest since the specimen described above was collected at the same locality and from the same bed as *Mooreoceras* sp. undet. 1. *Pseudorthoceras* has also been found in the calcareous black shale of the Cherokee of Kansas (Williams, 1937).

Measurements.—Length of fragment, 4.5 mm.; greatest width, 2.5 mm.; smallest width, 2.3 mm.

Locality.—Dover P-3.

Figured specimen.—State University of Iowa, 1944.

Genus MOOREOCERAS, Miller, Dunbar & Condra, 1933

MOOREOCERAS sp. undet. 1

Plate 50, figure 16

Fragment of a small narrow and straight conch that gradually expands orad, is slightly depressed and in cross section appears subcircular. Surface of internal limonitic mold smooth and bears faint transverse markings which appear to be regularly spaced. Septa simple discs gently convex apicad. Sutures nearly straight. Seven camerae occupy a space of approximately 1.2 mm. Within this space the shell expands orad from 1.8 mm. to 2.0 mm. Nature and position of siphuncle unknown.

Remarks.—A single fragment is available. It is of interest that *Mooreoceras bakeri* Miller and Dunbar occurred in the Burlingame limestone of Lyon County, Kansas (Miller, Dunbar and Condra, 1933: 93). The only other "Dry shale" fossil known from the Burlingame was the ostracod, *Hollinella gibbosa* (Tasch, this issue). The specimen described above appears to be closest to *Mooreoceras* spp. (Miller and Youngquist, 1949: 25–28, and plate 55, fig. 17). That specimen figured at natural size was 15 mm. long and tapered from 4.0 mm. to 5.0 mm. within that distance.

Measurements.—Fragment of conch. 4.1 mm. long, expands from 1.5 mm. to 1.8 mm. within that distance.

Occurrence.—Locality Dover P-3.

Figured specimen.—State University of Iowa, 1943.

Genus METACOCERAS Hyatt, 1883

METACOCERAS sp. undet. 1

Plate 50, figures 11, 12, 15

Three fragments of a subdiscoidal conch, whorls expand orad, approximately subquadrate in cross section; slightly concave laterally; ventral surface of limonitic internal molds bear on either side an en-echelon series of faint, narrow welts that generally trend apicad; the parallel welts on either side are joined across the median sector by concave extensions; the median sector of the ventral surface is traversed by a lirate-type single line; ventrolateral zone of conch nodose; distance between apices (on one fragment) of two preserved nodes, 1.5 mm.; area between nodes on lateral surface concave; flanks of nodes end abruptly at dorsum; two parallel, short and central, vertical depressions occur on the dorsum; sutures form broad shallow lateral lobe, shallow-to-almost straight ventral lobe; siphuncle small, subcentral.

Measurements.—Dimensions of the three fragments are:

Length (mm.)	Greatest Width (mm.)	Least Width (mm.)	Visible Segments
4.0	4.5	3.5	—
4.0	5.0	4.8	2
8.8	8.5	7.0	—

Locality.—Dry E-1, E-1a.

Figured specimen.—State University of Iowa, 1941.

METACOCERAS sp. undet. 2

Plate 50, figures 9, 10

Single fragment of a limonite internal

mold showing two camerae within length of 2.7 mm.; subtrapezoidal in outline. Sutures form shallow (almost straight) ventral lobe and a more concave lateral lobe; very shallow sinus and traces of welt-like ornamentation on ventral surface; siphuncle small, subcentral.

Remarks.—This species differs from *Metacoceras* sp. undet. 1 in that its outline is more nearly subtrapezoidal than subquadrate; in the absence of the slight lateral concavity and the presence of a very shallow but distinct ventral sinus.

Measurements.—Length of fragment, 2.7 mm.; least width, 3.8 mm.; greatest width, 4.0 mm.

Locality.—Dover P-2.

Figured specimen.—State University of Iowa, 1942.

Genus IMITOCERAS Schindewolf, 1923

IMITOCERAS GRAHAMENSE (Plummer & Scott)?

Plate 50, figures 3–6

Aganides? sp. ELIAS, 1936, Internat. Geol. Cong., Rept. 16th sess., vol. 1, p. 695.

Neoaganides grahamensis PLUMMER & SCOTT, 1937, Texas Univ. Bull. 3701, pp. 18, 350–351, 390, 502, text. fig. 88 (opp. p. 402), pl. 40, figs. 4–9.

Imitoceras grahamense MILLER & OWEN, 1939, Jour. Paleontology, vol. 13, pp. 146–147, text fig. 2, pl. 20, figs. 18–20; MILLER & UNKLESBAY, 1943, idem, vol. 17, pp. 11–12; SHIMER & SHROCK, 1944, Index fossils of North America, p. 573, pl. 234, figs. 18, 19; MILLER & DOWNS, 1950, Jour. Paleontology, vol. 24, pp. 185–218, text fig. 2, pl. 32, figs. 1–4.

The single specimen found among hundreds of imitoceratids from the same locality, resembled *Imitoceras grahamense*

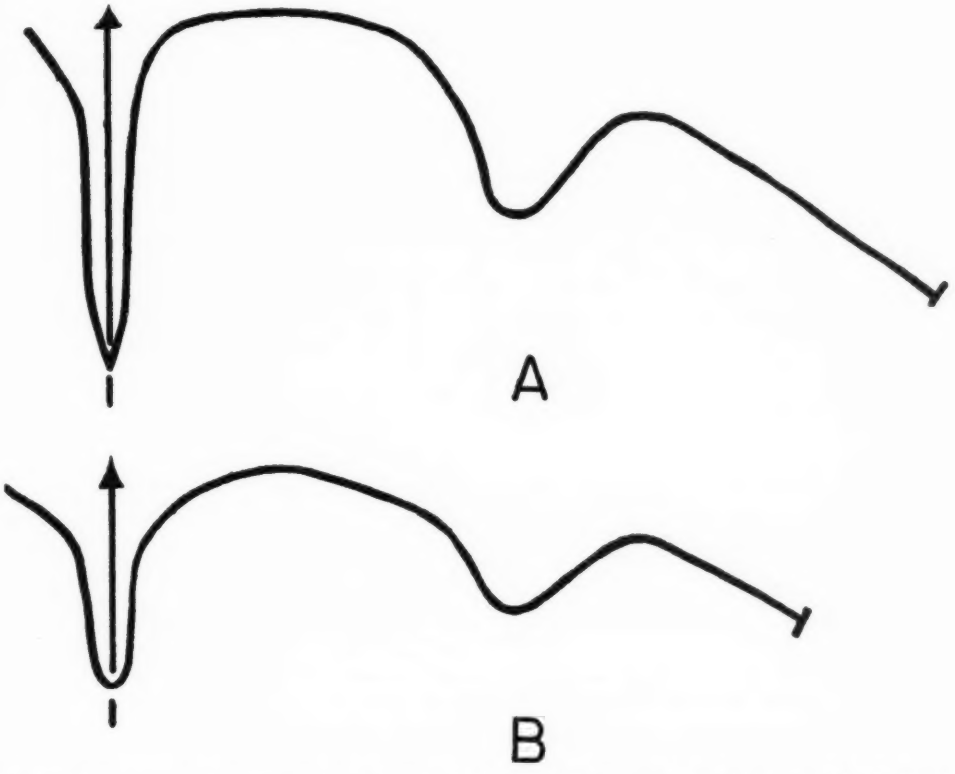

FIG. 1—Diagrammatic representations of part of the external sutures of two imitoceratids. A. Portion of most adoral suture of *Imitoceras grahamense*? where diameter of conch is 3.0 mm. Compare elongation and taper of ventral lobe with that of *I. grahamense*, ×50. B. Portion of external suture of *Imitoceras grahamense*, ×42.

(Plummer and Scott) in every way except in the character of the ventral lobe. As originally described by Plummer and Scott (1937: 350–351) for *Neoaganides grahamensis* (=*Imitoceras grahamense*) the ventral lobe is "long, narrow and rounded posteriorly."

Miller and Downs (1950: 193) describe mature sutures of this form as consisting of a "rather narrow spatulate rounded ventral lobe." For the specimen at hand the ventral lobe is about twice as long as usual, distinctly narrower than usual and tapers to a sword-like point rather than being spatulate in shape and rounded posteriorly. Study of a large collection of *Imitoceras grahamense* did not reveal any immature or mature sutures of this type. It may further be observed that all visible sutures of the specimen under discussion have the same tapered ventral lobe.

Based on suture spacing, all of the visible sutures of the specimen are interpreted to be immature.

Discussion.—Two factors stand out relative to the specimen described above. First, there is no evidence in any imitoceratid studied in the relatively large collections available of any comparable shape of the ventral lobe of the suture. Second, this specimen is identical with *I. grahamense* in every respect except shape of the ventral lobe of the suture. In light of these factors, it can be classified tentatively as a mutant individual.

Dimensions.—Maximum diameter, 3.3 mm.

Locality.—Dry E-1a.

Figured specimen.—State University of Iowa, 1945b.

Genus EOASIANITES Ruzhencev, 1933

EOASIANITES sp. undet. 1

Plate 50, figures 7, 8

Form subglobose, moderate expansion of conch orad; umbilicus deep, width slightly more than one-third diameter of specimen, umbilical shoulders rounded. Surface of conch marked by faint fine transverse lirae. Trace of umbilical ribs or tubercles. Three constrictions on last whorl, not too deeply incised. The external suture consists of a wide ventral lobe and on each side of it, two saddles and one lobe; the second saddle is on the umbilical shoulder. The ventral lobe is divided by a narrow median saddle which, in the most adoral suture, is more

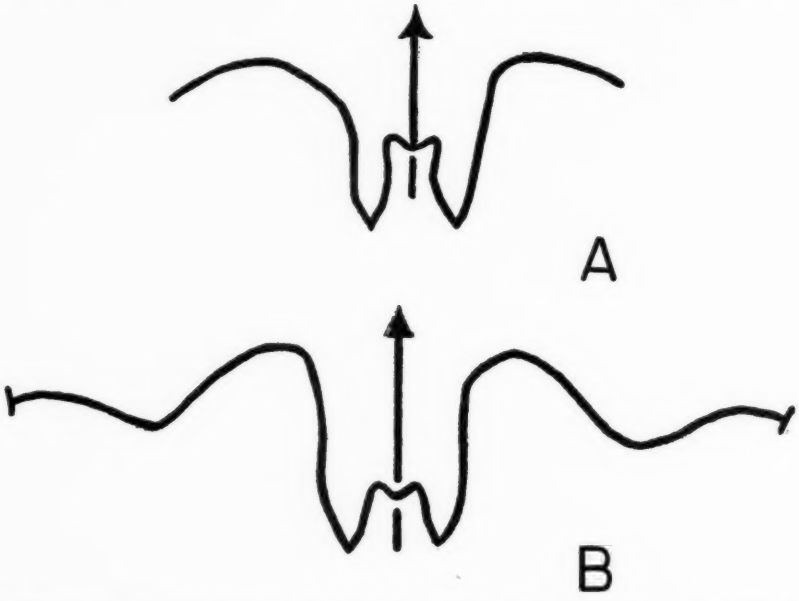

FIG. 2—Diagrammatic representations of external sutures of *Eoasianites*, sp. 1, ×22. A. Ventral lobe of the most adoral suture. B. Shape of suture where conch is 6.5 mm. in diameter.

than half as deep as the lobe is long. The sides of the median saddle are straight in all sutures but the most adoral where it is gently concave; it is divided centrally by a shallow tertiary lobe. The two lateral subdivisions of the ventral lobe are narrower than the intervening saddle, almost parallel and taper to nearly pointed apex. The first lateral saddle is broad and rounded; the saddle on the umbilical shoulder is broad and shallow as is the first lateral lobe.

Remarks.—The most adoral suture has a ventral lobe which is quite close to *Gastrioceras listeri* (Martin) (cf. Plummer and Scott, 1937: plate 13, fig. 4). In other respects these two species differ as follows: the above species has a first lateral lobe which is not V-shaped; in *G. listeri* umbilical width is greater and ornamentation more pronounced.

Septal spacing indicates an immature growth stage for the limonitic mold of the species described above.

Dimensions.—Maximum diameter, 7.6 mm.

Locality.—Dover P-1.

Figured specimen.—State University of Iowa, 1946.

EOASIANITES sp. undet. 2
Plate 50, figures 1, 2

Form subglobose, moderate expansion of conch orad; umbilicus deep, width slightly less than one-half diameter of specimen, umbilicus approximately twice as wide as deep. Umbilical shoulders rounded. Each volution of conch is marked by three rounded transverse constrictions which are moderately sinuous; as these cross the ventral zone, they curve slightly orad. Numerous transverse ribs occur on the umbilical wall of the outer volution and proceed across ventral zone.

The external suture consists of a broad ventral lobe and on each side of it two saddles and one lobe; on the umbilical wall faint traces of an additional lobe occur. The ventral lobe is more than twice as wide as long and its sides deviate from the vertical and are concave outward; it is divided by a short broad median saddle which is one-half as deep as the lobe is long and is almost straight on the sides and divided centrally by a small saucer-like tertiary lobe. The two lateral subdivisions of the ventral lobe are narrower than the intervening saddle and taper within a short distance to a nearly pointed apex. The first lateral saddle is narrower than the ventral lobe and asymmetrically U-shaped. The lateral lobe is broad, short and tapers to a narrow roundness. The second lateral saddle is broad, shallow, asymmetrical. The internal suture is not visible.

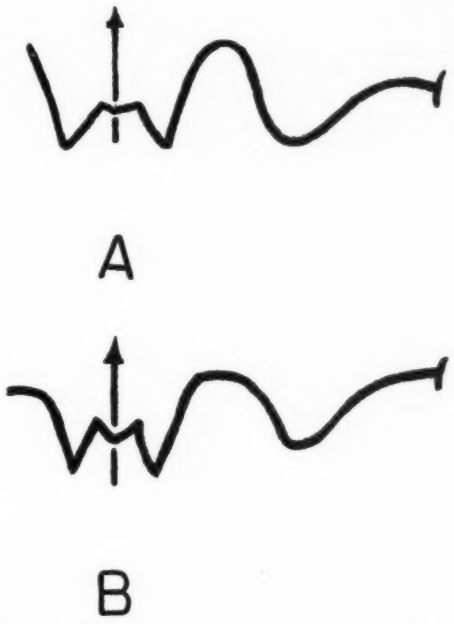

FIG. 3—Diagrammatic representations of portions of the external sutures of *Eoasianites* sp. 2, ×24. A. Portion of suture showing shape of ventral lobe where diameter of conch is 4.8 mm. B. Shape of portion of most adoral suture.

Remarks.—This species differs from *Eoasianites* sp. undet. 1 in the characteristics of the ventral lobe of the suture, the more pronounced subangularity of the first lateral lobe, greater umbilical width, and depth. It appears to resemble *G. drakei* A. K. Miller particularly in the characteristics of the ventral lobe and first lateral lobe of the external suture, but differs from that species in the absence of distinct nodes on the umbilical shoulder from whence issue fine costae, in the shape of the first lateral lobe, as well as in the greater depth of the median saddle of the ventral lobe, and in the ab-

sence of subangular umbilical shoulders.

Discussion.—A few observations may be made on the constrictions. These are not crossed by costae but are traversed by two successive sutures. The constrictions on the limonitic mold which in the original shell represented an area of heavier calcium carbonate deposition, may represent an adaptive modification of ornamentation (ribbing) for purposes of buoyancy or strengthening of the shell. Thus, an area which two or three narrow, shallow ribs ordinarily traverse on the shell, becomes an area of excessive deposition forming a super-rib. The fact that two sutures traverse the constriction on the limonitic mold suggests that this super-rib was formed after the septa of which the sutures are a peripheral trace, had been laid down.

Occurrence.—Dover P-1.

Dimensions.—Maximum diameter, 5.9 mm.

Figured specimen.—State University of Iowa, 1947.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 451–455, 7 TEXT FIGS., MAY 1953

A STUDY OF THE POLYMORPHIC SPECIES *GLYCYMERIS AMERICANA**

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ABSTRACT—The polymorphic species *Glycymeris americana* had a distinctive mutant rugose, which was found only in late Miocene populations of the species. The mutant trait rarely appeared on shells of less than 10.0 mm. in height, which was from 10 to 14% of the average adult shell size.

INTRODUCTION

DEFRANCE in 1826 described *Glycymeris americana* as *Pectunculus americanus* from fossils collected in North Carolina. His description was generally overlooked by American workers, and for the next 70 years many different names were applied to this species—*pulvinata* Lamarck, *lentiformis* Conrad, *tricenarius* Conrad, *quinquerugata* Conrad, *passus* Conrad, *elephantopus* Lea, *carolinensis* Holmes (not *carolinensis* Conrad), *undata* Linné. The types of Conrad's species were examined to make certain of some of the above synonyms. For a more detailed but less accurate synonymy, see Dall (1898, pp. 609, 610) or Gardner (1943, pp. 28, 29). The numerous synonyms for *G. americana* arise from two main causes—changes in shell characters due to age and variations within the species.

Glycymeris americana is a large species as compared with most members of the Glycymeridae. The largest Recent specimen I have examined is 90.7 mm. high and 97.7 mm. long, but most specimens are considerably smaller; few attain three-fourths this size. The largest Pliocene specimen I have measured is 108.6 mm. high and 113.3 mm. long, and the largest Miocene specimen examined is 87.3 mm. high and 91.2 mm. long.

Glycymeris americana shows a great amount of variation. Some of this variation is due to differences in shell size; the radial ribs flatten as the shell gets larger. Some variation is due to environmental factors, as for example the thickness of the shell. Most of the variation, however, is probably due to genetic factors. Some Pliocene specimens have a pronounced subtrigonal outline. The most interesting and distinct variant is what I will call the mutant rugose. This mutant was given the species name *quinquerugata* by Conrad. Dall (1898, p. 610) and Gardner (1943, pp. 27, 28) synonymized *quinquerugata* with *americana*.

Because it is unusual and can be readily distinguished, the mutant rugose is the main topic of this paper.

More than 700 specimens of *Glycymeris americana* were examined and measured.

HISTORY OF *GLYCYMERIS AMERICANA*

Glycymeris americana first appears in strata of late Miocene age in Virginia. On the basis of shell morphology, the nearest related species is *G. parilis* (Conrad) from the middle Miocene of Maryland. A species morphologically similar to *G. parilis* was the progenitor of *G. americana*. During the late Miocene *G. americana* was common in Virginia, North and South Carolina, Georgia, and Florida (figure 3). In the Pliocene this species did not occur north of Cape Hatteras, but was abundant in southern North Carolina and South Carolina. It appears to have been less common in the Pliocene of Georgia and Florida (figure 2). The relative restriction of distribution of *G. americana* in the Pliocene may be due in part to the incompleteness of the geologic record. It seems, however, that *G. americana* reached its acme of development in the latest Miocene. At present *G. americana* is found from Cape Hatteras southward and around Florida at least as far west as Destin, Okaloosa County (figure 1). No glycymerid

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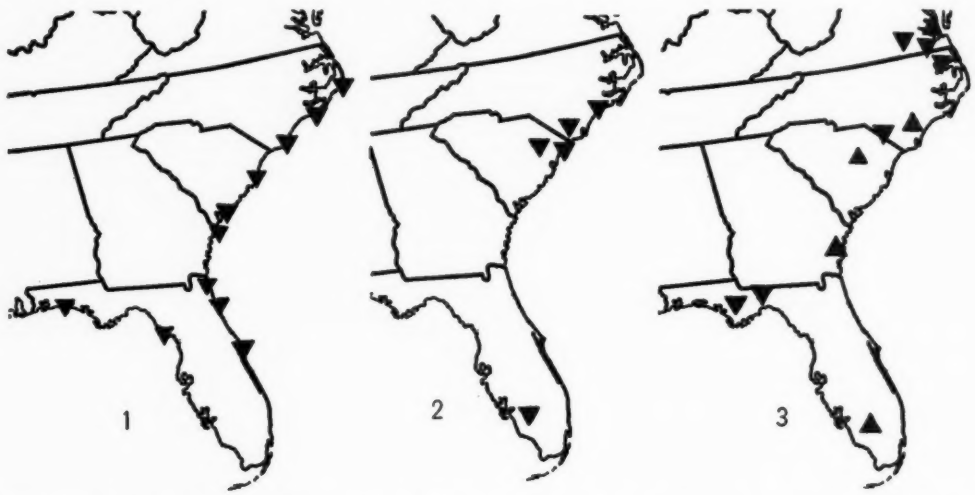
has been reported living north of Cape Hatteras in the western Atlantic.

From the brief account of geographic distribution, it appears that *Glycymeris americana* spread rapidly southward from its place of origin (probably in or near Virginia) throughout the Miocene. There seems to have been a slight contraction of its range during the Pliocene, and its range appears to have remained relatively constant since that time. The rapid expansion of range and of number of individuals took place within a period of about 4,000,000 years. The period of slight contraction and later constancy of range has lasted about 11,000,000 years. This species, therefore, has been in existence for about 15,000,000 years.



FIGS. *1–3*—Maps of southeastern U.S. showing distribution of *Glycymeris americana* (Defrance). *1*, Recent; *2*, Pliocene; *3*, Miocene. ▼ Localities where only normal forms occur. ▲ Localities where both normal and rugose forms or only rugose forms occur.

Most specimens of *Glycymeris americana* at the U. S. National Museum have been dredged from a sandy bottom. The depths at which specimens have been collected range from 15 to 160 meters but most commonly range from 15 to 65 meters. Of the 30 records, only one indicates a depth greater than 65 meters.

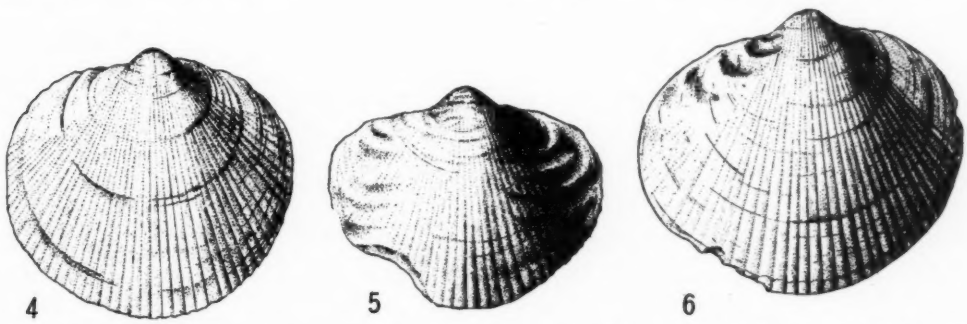
Glycymeris americana appears to be nearly extinct. The reasons for this statement are: 1. Recent specimens are relatively rare, and very few of them are found alive. Many, in fact, have obviously been dead for a long period, as the shells are badly worn. 2. Very few full-grown Recent specimens are found. 3. Recent specimens show little variation as compared with fossil representatives. 4. Although *G. americana* occupies nearly the same range as it did millions of years ago, its occurrence now is relatively spotty.

THE MUTANT RUGOSE

The rugose form has folds on the posterior side of the umbo (figure 6). These folds may be so pronounced that they are reflected on the interior of the shell along the posterior and posterior dorsal sides. This reflection of the exterior folds is best seen on small or medium-sized shells. A few specimens have folds on the anterior and posterior sides of the umbo, but those on the anterior side are usually less pronounced than those on the posterior side. Even more rarely, a specimen will have rugae on only the anterior side of the umbo. Rugae appear in shells as small as 7.0 mm., in height, but this mutant trait does not ordinarily develop in shells of less than 10.0 mm. in height. In other words, the mutant shows its effect when the shell has attained one-seventh or about 14% of its adult size (70.0 mm.). This is a conservative estimate; perhaps 10% would be more nearly correct. The largest number of rugae observed on the posterior side of the umbo was eight, on the

anterior side of the umbo four. Although there are more than 650 described species of glycymerids, I have observed rugae in only two of them—*Glycymeris americana* and *G. aberrans*.

Dall (1898, p. 611) had the following to say about the rugose mutant.



FIGS. *4–6—4, Glycymeris americana* (Defrance), exterior, normal form, upper Miocene, Duplin formation, Natural Well, Duplin County, North Carolina, Hypotype USNM 561491; *5, G. aberrans* Nicol, exterior, upper Miocene, Dade County, Florida, Hypotype USNM 561486; *6, G. americana* (Defrance), exterior, rugose mutant, upper Miocene, Duplin formation, Magnolia, Duplin County, North Carolina, Hypotype USNM 561490.
All figures ×1⅛.

> The only form which may possibly be varietal, but which I am inclined to refer to some pathologic cause, is *G. quinquerugata*. This is almost entirely confined to Duplin County, North Carolina. Well-marked specimens have on each dorsal slope, from the beaks laterally, three to six little irregular ripples, which are much more conspicuous in the young. These might indicate the presence of some parasite in the individual. They are never uniform or regular; some specimens have them only on one side, in others they are obsolete, and, finally, others do not have them; and between the normal *americana* and the *quinquerugata* without rugae there is absolutely no distinction to be made.

It is unlikely that the rugae were caused by a parasite, as suggested by Dall, because the rugose forms are just as large as the normal forms from the same locality, there is no damage to the shell, and the rugose forms disappeared at the end of Miocene time although the "host species" did not.

Dall's statement that there is no difference between the rugose forms and the normal forms other than the presence or absence of rugae is essentially correct. Careful measurements of nearly 100 specimens indicate, however, that the rugose forms may be less convex than the normal forms.

The earliest occurrence of *Glycymeris americana* is in the Yorktown formation in Virginia. Specimens showing the rugose mutant in Virginia are rare. Dall stated that rugose specimens are almost entirely confined to Duplin County, North Carolina; but beds of late Miocene age in North Carolina, South Carolina, Georgia, and Florida commonly have the rugose form of *G. americana*. Collections from Duplin County have been more extensive than from other areas which have rugose specimens. Table 1 lists localities of late Miocene age where *G. americana* was collected and shows the number of rugose and normal specimens observed in each locality. Only specimens 10.0 mm. in height or greater were included; smaller specimens rarely show rugae. The geographic distribution of the rugose mutant is shown in figure 3.

The earliest specimens of *Glycymeris americana* do not show the mutant trait; but as the Miocene epoch drew to a close, rugose specimens appeared. The mutant forms became more and more numerous in various populations until the end of the Miocene. They suddenly disappeared at the end of the Miocene, and only normal or nonrugose specimens appear in Pliocene and younger beds. At the end of the Miocene further mutations affected some rugose individuals, giving rise to the rare and short-lived species *G. aberrans* which has been reported from South Carolina and Florida (see figure 7 for probable phylogeny).

TABLE 1.—SHOWING UPPER MIOCENE LOCALITIES WITH PERCENTAGES OF RUGOSE FORMS

Locality	Formation	Rugose posterior	Rugose anterior	No rugae	% of rugose forms
Pampa, Va.	Yorktown	1	—	1	50
Petersburg, Va.	Yorktown?	—	—	5	00
Suffolk, Va.	Yorktown	—	—	5	00
Smithfield, Va.	Yorktown	—	—	5	00
Nansemond, R., Va.	Yorktown	—	—	18	00
Willis Lee's Wharf, Va.	Yorktown	—	—	13	00
Gaskin's Wharf, Va.	Yorktown	—	—	7	00
Chowan R., N. C.	Yorktown?	—	—	10	00
Magnolia, N. C.	Duplin	77	4	56	60
Kenansville, N. C.	Duplin	1	—	1	50
Mayesville, S. C.	Duplin	6	—	1	86
Brunswick R., Ga.	Duplin	4	—	—	100
Leon Co., Fla.	Choctawhatchee *Ecphora* Zone	—	—	13	00
Jackson Bluff, Leon Co., Fla.	Choctawhatchee *Cancellaria* Zone	—	—	3	00
Ortona Locks, Fla.	Choctawhatchee? *Cancellaria* Zone?	19	—	4	83

The rugose mutant was present in populations of *Glycymeris americana* for about 3,000,000 years or about 20% of its life span thus far.

Further studies of this type will no doubt show many polymorphic species of mollusks in the fossil record. In this case, and most certainly in others, mutants will aid stratigraphers in deciphering the age of strata.

ACKNOWLEDGMENTS

Mrs. Sally Lee made the drawings of *Glycymeris americana* and *G. aberrans*. Miss Anne Harbison showed me Conrad's type specimens at the Academy of Natural Sciences of Philadelphia. Mr. Wm. J. Clench allowed me to borrow for study Recent specimens of *G. americana* from the Museum of Comparative Zoölogy at Harvard College. I am greatly indebted to these persons for their help.

ADDENDUM

In a recent discussion, Dr. Richard E. Blackwelder of the U. S. National Museum raised the question as to whether the difference between rugose and normal forms of *Glycymeris americana* was continuous or discontinuous. He pointed out that if the variation is continuous, i.e., with all intermediate steps present, the species is not polymorphic.

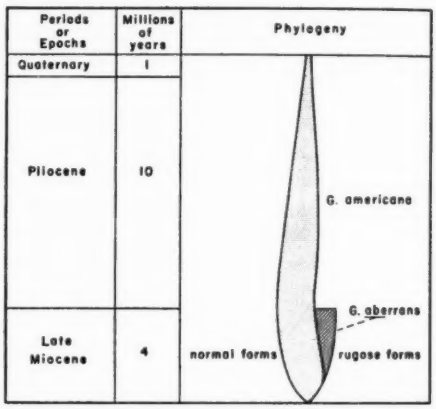


FIG. 7—Chart showing the relationship of *Glycymeris americana* and *G. aberrans* and the occurrence of rugose and normal forms of *G. americana*.

The number of rugae, where present at all, ranges from one to eight; however, the most common number is three or four. Only three of the specimens examined have one ruga, and all three of these are small shells, not more than 11.0 mm. in height. Of 19 specimens having two rugae, only two shells are large, about 70.0 mm. in height. All specimens having six or more rugae are

medium-sized or large. The conclusion is that there seems to be a definite correlation between size and number of rugae. As all adult rugose specimens have at least two rugae, the variation does appear to be discontinuous; but perhaps more data are necessary to ascertain whether *Glycymeris americana* is a polymorphic species.

MANUSCRIPT RECEIVED MAY 28, 1952

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NOTICE

CATALOGUE OF NORTH AMERICAN DEVONIAN FOSSILS

Unit 1-F, part B, comprising 39 cards on the family Chonophyllidae (Tetracoralla) has recently been published. It was prepared by Dr. E. C. Stumm under the auspices of the Paleontological Society, and is published by the Wagner Free Institute of Science, Philadelphia 21, Pennsylvania. It is available from the Institute at a price of $3.50 plus carriage.

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 456–470, 15 TEXT FIGS., MAY 1953

PERMIAN VERTEBRATES FROM TAYLOR COUNTY, TEXAS

JOHN ANDREW WILSON
University of Texas, Austin

ABSTRACT—Stratigraphic range of well-known Permian amphibians and reptiles is extended upward into the Vale formation, and their geographic range is extended southward into Taylor County, Texas. From the same locality and formation is described *Lawnia taylorensis*, a new genus and species of paleoniscoid fish.

INTRODUCTION AND ACKNOWLEDGMENTS

THE discovery of Permian vertebrates in Taylor County, Texas, in 1939 and 1940 was the first significant find of material at a stratigraphic horizon above the Arroyo formation. It extended the geologic range of certain members of the Arroyo fauna into the Vale formation and, in addition, has extended the geographic range of the Texas Permian vertebrate collecting localities 200 miles to the south. Several specimens of well-preserved paleoniscoid fishes and a large quantity of plant material were discovered associated with common well-known forms, such as *Trimerorhachis*, *Diplocaulus*, *Seymouria*, and *Dimetrodon*. Only the paleoniscoids will be described since the amphibians and reptilians add nothing new to knowledge of these forms. Later field work by Olson, for the University of Chicago, in Knox County, Texas, has disclosed a Vale fauna higher in the formation; the two collections in some respects supplement each other. The Taylor County collection is of further interest because most of it comes from a single quarry at one stratigraphic level and hence seems to be as close to a natural population as could be hoped for in vertebrate paleontological work.

The field work and most of the preparation of the specimens were completed in the state-wide Paleontological and Mineralogical Survey project of the Work Projects Administration sponsored by the Bureau of Economic Geology, The University of Texas, in 1939 and 1940. Major credit for the collecting and the over-all supervision of the project belongs to Dr. E. H. Sellards, then Director of the Bureau of Economic Geology, and to Mr. Glen L. Evans. The present Director of the Bureau of Economic Geology, Dr. John T. Lonsdale, (with whose permission this paper is published), made the material available and furnished financial support for this study. The author expresses his most sincere appreciation to these three gentlemen for their assistance and encouragement. Grants-in-aid from the University Research Institute defrayed the cost of illustrations. The writer is indebted to Mrs. William A. Clark and Miss Grace E. Hewitt for their efforts spent in preparing the drawings.

LOCATION

The material described was collected from the southern part of Taylor County, Texas, in the SW ¼ of section 436 of the M. P. King survey, on the property of Mr. C. O. Patterson, Route 1, Lawn, Texas. The land was leased to Mr. Sid McAdams at the time the collection was made, and the specimen labels bear the locality notation "Sid McAdams Lease." The main quarry site, Site 7, is located about 6 miles southwest of the small town of Lawn.

To reach the quarry site by car: Starting from in front of the theatre in Lawn, go 1.5 miles west, turn south and go 2.9 miles, turn west and go 1.1 miles, turn south and go 0.5 mile to the home of Mr. C. O. Patterson. The quarry dump is in a pasture against the east slope of a prominent but low hill and may be seen west-southwest from the west side of Mr. Patterson's house.

Olson (1948) suggested a method of designating localities by means of coordinates on aerial photographs. His method is followed here except that instead of measuring from the lower right-hand corner, the principal point is determined from the collimation marks and measurements are made from there. The W.P.A. quarry, Site 7, has the

following designation:

Soil Conservation Service Photograph CLO-2-135
From principal point . . . . . $3\frac{7}{8}$ inches east, $4\frac{7}{8}$ inches south
Scale: 4 inches equals 1 mile.

GEOLOGY AND STRATIGRAPHY

The Bureau of Economic Geology has published a preliminary geologic map of Taylor County (Meyers and Morley, 1929) which was compiled from various oil company maps. Using this map and aerial photographs, the writer compiled data for a geologic map to cover the area of the quarry site. It was found that the quarry is approximately 22 feet above the Vale-Standpipe contact.

Measured sections in Taylor County vary from place to place, as do sections measured in the Permian red beds to the north. Traceable beds are not persistent over wide areas so the quarry section can be interpreted as having only very local significance. (See Case, 1919, for descriptions of Permian sections in Archer and Baylor counties.)

The proximity of the quarry to marine formations of known age permits a more exact dating than has been possible in many areas to the north. In the upper portions of the Arroyo formation in Taylor County there is an alternation of marine and continental sediments. The marine phases are recognized by limestone members which are in many places fossiliferous. The continental facies are represented by unfossiliferous red, green, and brown shales and thin sands. The limestones vary from an inch to 2 feet thick, whereas the continental beds are usually 3 to 10 feet thick. During Vale time, continental conditions dominated, and the almost continuous section of red shales reaches a thickness of about 340 feet (Wrather, 1917) before the next marine bed, the Bullwagon dolomite, appears. The southern advance of continental conditions as one goes up the stratigraphic section has long been surmised, but it is now well substantiated by the discovery of land vertebrates at this position.

ENVIRONMENT OF DEPOSITION

The association of vertebrate, invertebrate, and plant remains in Site 7 presents an unusual chance to interpret the local environment. A collection of several different types of the plant remains found in the quarry was sent to Dr. C. A. Arnold of the Department of Botany, the University of Michigan. Dr. Arnold was able to make the several determinations as follows:

Taeniopteris multinervis
Walchia sp.
?Odontopteris sp.

The plants listed were recovered from a gray section of the red siliceous clays.

The pelecypods which were recovered from a stream-channel conglomerate lying within the red and gray siliceous clays were sent for identification to Dr. N. D. Newell of The American Museum of Natural History and Columbia University. Dr. Newell replied that they were fresh-water forms belonging to the family Anthracosiidae and provisionally referred them to the genus *Palaeanodonta*. The author is grateful to both Dr. Arnold and Dr. Newell for their kind assistance.

The vertebrates are fresh-water and dryland forms. The former are represented by the paleoniscoid fish and by *Trimerorhachis* and *Diplocaulus*, amphibians. *Trimerorhachis* bones are most common in the conglomerate beds. *Seymouria*, an intermediate form between the amphibians and the reptiles, and the reptile *Dimetrodon* represent the shore dwellers of the assemblage. Their remains, except for occasional isolated bones of *Dimetrodon* found in the conglomerate, are confined to the fine-grained sediments.

X-ray analyses of the siliceous clays, made by the Research Laboratory in Ceramics of The University of Texas, show that the gray siliceous clay is composed chiefly of quartz, about 60 to 70 percent. The remainder of the sample is composed of a mixture of halloysite with rather abundant glauconite. Analysis of the red siliceous clays shows only the addition of hydrohematite. The limestone, clay pebble conglomerate is composed mostly of calcite with a very small percent of dolomite. This material also contains 5 to 10 percent quartz and a trace of orthoclase feldspar. The only heavy mineral noted in this sample is hydrohematite. The clay portions of this sample

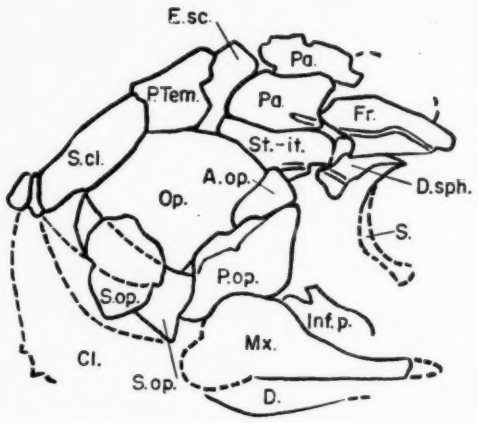

FIG. 1—B.E.G. no. 30966-403, *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Outline of internal surface of bones of posterior and lateral portions of right side of skull. Bone impressions shown by dashed lines. ×2. Abbreviations used on this and succeeding figures are listed on p. 470.

are of the same composition as that previously mentioned.

The local environment seems to have been a low delta or flood plain occupied by quiet pools or lakes and traversed at times by swifter running streams. The evenly bedded, siliceous clays must have been deposited in very still water whereas the limestone, clay pebble conglomerate which pinches out laterally must have been laid down in streams of running water.

The sediments appear to have been derived from siliceous and lime-bearing rocks to the east. It is very possible that they were derived from the now buried portions of the Ouachita Mountains.

DESCRIPTION OF THE PALEONISCOID MATERIAL

The most important part of the fauna from Taylor County consists of the well-preserved remains of 16 specimens of a new paleoniscoid fish. They are preserved as flattened specimens in soft gray or red clay; the bone is light brown. The individual fish are in various stages of disarticulation; two are almost complete and are preserved in counterpart; others are almost complete but scattered over the surface of the blocks. There are four well-preserved skulls from which it is possible to construct a reasonably accurate restoration. Two of the specimens were cleaned by members of the W.P.A. staff of preparators; the remainder were cleaned by the writer, using a fine needle under a high-magnification binocular microscope.

SYSTEMATIC DESCRIPTION

Order PALEONISCOIDEA

Family AMBLYPTERIDAE

Genus LAWNIA Wilson, new genus

Characters.—Suspensorium nearly vertical, teeth small, oral border of maxilla slightly deflected, posterolateral border of frontal notched for supratemporo-intertemporal, double row of supra-orbital bones, slightly overhanging rostrum, scales rhomboidal and smooth with smooth posterior margins, dorsal fin large and opposite posterior end of pelvic fin, fulcra small.

Type species.—*Lawnia taylorensis* Wilson, new genus and species.

LAWNIA TAYLORENSIS Wilson, n. sp.
Text figures 1–15

Type.—B.E.G.[1] no. 30966-400: a laterally compressed fish with skull, body, fins, and tail; preserved in counterpart.

Hypodigm.—B.E.G. no. 30966-244: a laterally compressed fish with body, fins, and tail, skull lacking rostral elements; preserved in counterpart.

B.E.G. no. 30966–401: a laterally com-

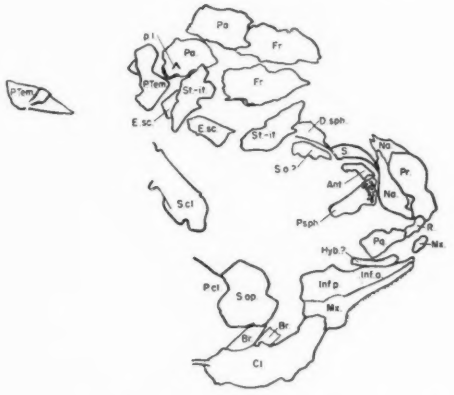

FIG. 2—B.E.G. no. 30966–401. *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Outline of bones of skull as preserved. ×1.

[1] Bureau of Economic Geology, The University of Texas.

pressed fish without fins or tail, skull bones scattered.

B.E.G. no. 30966-9: a laterally compressed skull lacking only the posterodorsal portion of the skull but with the bones displaced; impression of the anterior portion of the body preserved in counterpart.

B.E.G. no. 30966-403: a laterally preserved skull with well-preserved internal surfaces of the cheek bones and anterior portion of the body.

B.E.G. no. 30966-402: a laterally compressed body with well-preserved dorsal, anal, and caudal fins and showing the dorsal and ventral ridge scales.

Geological horizon and locality.—Approximately 22 feet above the base of the Vale formation, Clear Fork group of the Leonard series of the Permian, in the SW ¼ of section 436, M. P. King survey, Taylor County, Texas, on property now owned by Mr. C. O. Patterson, Route 1, Lawn, Texas.

Dermal bones of the dorsal side of the skull (*fig. 7*).—The relationships of the post-temporals can be best determined from specimen no. 403 (fig. 1). The bones resemble the shape of right triangles with the hypotenuse of each triangle forming its median borders. The right and left bones are in contact for about 1 mm. along the median line, and posterior to this they separate at an angle of about 55° (measured from the median line). Their posterior corners are not crenulated as in *Brachydegma* (Dunkle, 1939, fig. 1) but form a blunt point. Posterolaterally the post-temporal overlaps the supracleithrum and anterolaterally suturates with but does not overlap the operculum. In turn, the post-temporal is over-

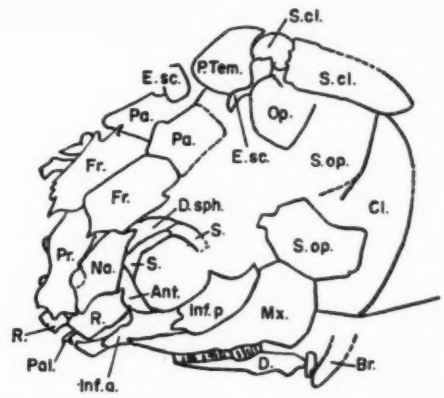

FIG. 3—B.E.G. no. 30966–400, *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Outline of bones of skull of type. ×1.8.

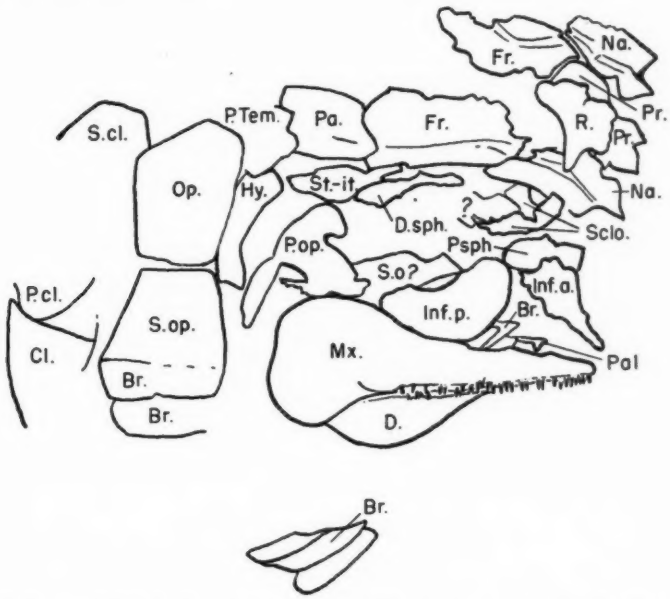

FIG. 4—B.E.G. no. 30966-9, *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Outline of bones of skull as preserved. ×2.

lapped along its entire anterior border by the extrascapular. A small fracture in the left post-temporal on specimen no. 403 reveals the course of the sensory canal close to the lateral border.

The extrascapulars are oblong shaped, approximately three times as wide as long. The left extrascapular in specimen no. 403 (fig. 1) is the best preserved and is seen from the ventral surface. It is a single bone exactly as broad as the anterior end of the post-temporal. Anteriorly it is as broad as the combined widths of the posterior margins of the parietal and the supratemporo-intertemporal, both of which overlap it. Laterally the extrascapulars meet the operculum. Faint ridges on the ventral surface of the extrascapular indicate the courses of the sensory canals.

The parietals (figs. 1, 3) are longer than wide. They are very thin along the median suture and gradually thicken laterally. The thickest portion underlies the pit lines and the posterior part of the supra-orbital canal. The median suture is almost straight except for one open S-shaped curve opposite the pit lines. Anteriorly the parietals are overlapped by the frontals. The greatest extension of the parietals under the frontals occurs on the course of the sensory canal. At this point the two bones seem to interlock with a firm suture. The parietals are bounded along the entire lateral margins by the supratemporo-intertemporals.

The frontals (figs. 2–4) are almost twice as long as they are wide. Their median suture is more irregular than that of the parietals. In specimen no. 401 (fig. 2) the dorsal surface of the right frontal is shown alongside the ventral surface of the left frontal. From this specimen it can be clearly seen that the anterior part of the left frontal overlay the right, and conversely the posterior part of the right overlay the left. The posterolateral corners of the frontals are notched to receive an anteromedial process of the supra-temporo-intertemporal. Anterior to this notch the frontal is bounded by a straight suture with the dermosphenotic. Anteriorly the frontals wedge themselves between the nasals and the post-rostral. The supra-orbital sensory canal forms a ridge on the ventrolateral surface of the frontal which must have considerably strengthened the bone.

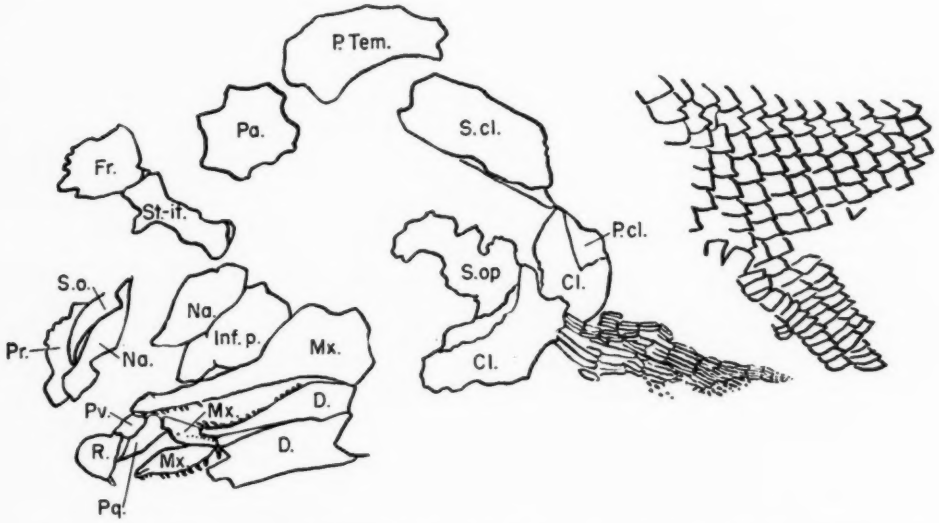

FIG. 5—B.E.G. no. 30966-180, *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Outline of bones of skull and anterior body scales to show lateral line. ×2.

The supratemporo-intertemporal is well shown on specimens no. 401 (fig. 2) (external) and no. 9 (fig. 4) and no. 403 (fig. 1) (internal). The latter two specimens show the right bone in an almost undisturbed position next to the parietal and frontal. The posterior margin of the supratemporo-inter-

temporal overlaps the anterolateral half of the extrascapular. The suture appears to be almost at right angles to the midline. The supratemporo-intertemporal is bounded on its medial side by the parietal and frontal. An anteriorly directed process fits into the excavated posterolateral margin of the frontal (fig. 7). The anterolateral margin of the supratemporo-intertemporal suturates with the posteromedial margin of the dermosphenotic. None of the specimens in the collection show exactly what bone joins the posterolateral margin of the supratemporo-intertemporal, although without doubt it was a suborbital. Close to the median lateral edge of the supratemporo-intertemporal is a low ventral lamina which forms a crescent-shaped ridge. There does not seem to be a notch (as in *Glaucolepis;* see Nielsen, 1942, p. 119, figs. 19, 20, 22, 23, 26, and pl. 12, fig. 2) below the vertical lamina. The vertical lamina in *Lawnia* is highest at its anterior end and slopes gently in a posterior direction. The relationship of this lamina to the *fossa bridgei* or to the *fossa hyomandibularis* cannot be determined since the neurocranium is entirely lacking. Posterior to the vertical lamina and at right angle to it and the long axis of the bone is another vertical lamina. This is much shorter than the first and rises from a thickened posterior extension of the aforementioned lamina.

The nasals are long, somewhat triangular-shaped bones. They overlap posteriorly the anterior margins of the frontals and dermosphenotics. Anteromedially they join with the post-rostral. Both the post-rostral and the nasals have opposing notches for the median nares. Ventral to the median nares the nasals again contact the post-rostral so

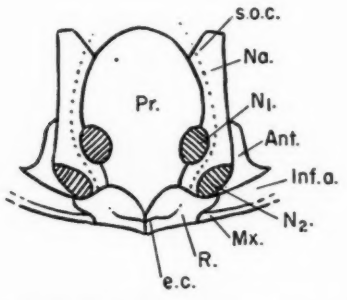

FIG. 6—Attempted restoration to show relationship of the bones of the snout. *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×2.

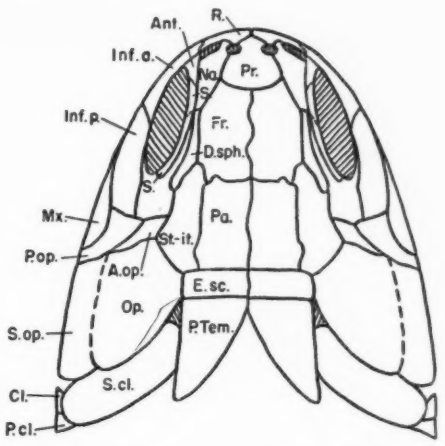

FIG. 7—Attempted restoration of the bones of the dorsal surface of skull. *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×1.6 circa.

that the more median nareal opening is entirely surrounded by these two bones. The anterior tip of the nasals appears to be overlapped by the rostrals. The anterolateral margins of the nasals are deeply notched for the lateral nares. The anterior ends of the nasals are perfectly preserved in specimens no. 9, 180, 400, and 401 (figs. 4, 5, 3, 2). Laterally the nasals overlap the antorbitals.

On the lateral edge of the dorsal side of the skull, posterior to the nasals and anterior to the supratemporo-intertemporals lie the dermosphenotics. Medially they suturate against the frontals and supratemporo-intertemporals. Laterally they probably joined a suborbital which is missing in all specimens.

Bones of the lateral portion of the skull (fig. 8).—The broad thin bones of the opercular series are poorly preserved in all specimens. In none of them can the writer be sure of the position of the suture between the operculum and the suboperculum. In the impression of specimen no. 9 (fig. 4), the change in direction of the ornamentation gives the approximate boundary. If the restoration is correct, the operculum is pentagonal in shape and slightly smaller than the suboperculum. The suspensorium as a whole is nearly vertical. At its anteromedial margin the operculum is overlapped by a small triangular-shaped antoperculum which forms a wedge between it and the pre-operculum. So little of both the opercu-

lum and the suboperculum is preserved that nothing more can be added to their descriptions.

Specimen no. 403 (fig. 1) is the only one in which the pre-operculum is well preserved. It is typically fan-shaped with a ventral process extending between the posterior-expanded end of the maxillary and the suboperculum. Dorso-anteriorly it expands until its height is greater than that of the orbit. Its anteroventral margin is overlapped by the posterior infraorbital. Its anterodorsal margin must have met one or more suborbitals which are not present.

A hyomandibular is exposed in approximately its normal position in specimen no. 9 (fig. 4). The ventral end is concave and was probably filled by a cartilaginous plug for articulation with the symplectic. (No symplectic was found in any of the specimens.) From its ventral end the hyomandibular seems to expand dorsally, although its full width cannot be determined because the posterior border is covered by the operculum.

Displaced branchiostegal rays (figs. 2–4) are present in several specimens. None of them is complete, however, so it is impossible to be certain of their exact length and number. In none of the specimens were any of the gular elements preserved, so that an attempt to restore the ventral aspect of the skull would be valueless.

The maxillary is a heavily ornamented bone of typical paleoniscoid shape with a very slight downward tilt to the posteroventral margin. Dorsally the maxillary is overlapped by the anterior and posterior infra-orbitals. This overlap increases anteriorly until the anterior infra-orbital almost completely covers it at a point just beneath the lateral nares. The maxillaries do not meet at the midline. In specimen no. 401 (fig. 2), on the internal side of the maxillary there is a faint suggestion of a suture. If there is a suture then what the writer has shown as single maxillary may possibly include a supramaxillary. The thick ornamentation on the external side of the maxillaries in the other specimens prevents verification of this. A horizontal lamina on the internal side of the maxillaries parallels the ventral margin about 1 mm. dorsal to it. It extends from the anterior end of the bone to the center of the expanded posterior portion. Elsewhere the internal surface is perfectly smooth.

The infra-orbitals are well preserved in most of the specimens. They form the ventral and posterolateral rim of the orbits. The writer has refrained from numbering the infra-orbital bones because of the uncertainty of the total number, preferring, therefore, to call the two identifiable ones anterior and posterior respectively, using the terms in a descriptive sense only. Both of the bones are so heavily ornamented that the course of the suborbital canal is obscured. The posterior infra-orbital is crescent-shaped and overlaps the dorsal margin of the maxillary along the posterior part of the anterior process. The overlap of the anterior infra-orbital with the maxillary has already been described. The anterior end of the anterior infra-orbital suturates with the posterior margin of the rostral. The anterior end of the anterior infra-orbital and the anterior end of the maxillary terminate together against the rostral.

Specimen no. 400 (fig. 3) exhibits two supra-orbital bones which form the dorsal rim of the orbits. The posterior one articulates anteriorly with the anterior supra-orbital and the nasal and anterodorsally with the dermosphenotic. What it articulated with posterodorsally and posteriorly is unknown. It probably was with a suborbital. The antorbital forms the anteroventral margin of the orbit and the posterior margin of the lateral nares. It is preserved in almost its natural position in specimen no. 400 (fig. 3). The anterior end of the maxillary joins with the posterior end of the rostral to exclude the antorbital and infra-orbital from the margin of the jaw.

The anterior margin of the snout is formed by the rostrals. Specimen no. 400 (fig. 3) is a complete though flattened skull with the snout, a rare condition in specimens of paleoniscoids. The rostrals are about as high as they are long. Anteriorly they meet at the midline; ventrally they bear two or three teeth. Posteriorly they articulate with the anterior infra-orbital and their posterodorsal corner just touches the ventralmost point of the antorbital. The dorsal margin of the left rostral is obscured by the ventral margin of the nasal in specimen no. 400. Specimens no. 9 (fig. 4) and 180 (fig. 5), however, have the rostral preserved in such

a way that there is a minimum of doubt concerning the restoration of the snout (fig. 6). The posterodorsal margin of the rostrals forms the ventral rim of the lateral nares. The anterodorsal margin suturates with the nasals and the post-rostral.

Bones of the ventral surface of the skull.—In specimens no. 401 (figs. 2, 9) and 180 (fig. 5) the ossified anteromedial surface of the right palatoquadrate is exposed. From these specimens it can be determined that the anterior end is formed by a prominent knob. Posterior to the knob is a groove which leads posterolaterally. The palatoquadrate expands posteriorly in a dorsal direction. The posterior ending of the ossified portion appears to have been continued in cartilage because the external surface of the bone is continued beyond the posterior ending of the internal surface. No sutures are visible on the bone nor are any teeth present on the ventral surface.

A small flat bone lying dorsal to the palatoquadrate in specimen no. 180 (fig. 5) is thought to be a pre-vomer.

Specimen no. 401 exhibits the anterior end of the parasphenoid. The bone is incomplete but sufficient portions are preserved (fig. 2) to show that teeth were present anteriorly. The bone is smooth and narrow posteriorly. Specimen no. 9 shows what is believed to be the dorsal surface of the parasphenoid but it is so overlain by parts of other bones that nothing further can be contributed.

Bones of the pectoral arch.—Fragments of a supracleithrum are preserved in most of the specimens. The supracleithrum is an elongate oval-shaped bone with strong ornamentation. The post-temporals overlap the supracleithrum dorsally. Anteriorly the operculum and the posterodorsal corner of the subopercular overlap the supracleithrum. The supracleithrum in turn overlaps about three rows of body scales. Ventrally the supracleithrum overlaps the cleithrum and the post-cleithrum. The post-cleithrum is relatively larger than that found in *Brachydegma* (Dunkle, 1939, fig. 1-A). In *Lawnia* it is teardrop shaped with the narrow end dorsal. It is best shown as in specimen no. 403 (fig. 1).

Ornamentation of the skull bones.—Figure 10 shows the ornamentation of such skull bones as it is possible to illustrate. The post-rostral and the rostrals are covered with very numerous high tubercles. The tubercles become more widely spaced on the posterior part of the post-rostral. The tubercles on the ventral margin of the post-rostral are elongate and curved downward, forming a hook-like arrangement. Each tubercle is very finely striated parallel to the long axis of the tubercle. The tubercles in the center of the post-rostral are a little shorter and blunter and tend to be more erect. The very close spacing and the overhang of the tubercles made the cleaning of the external surface of such highly ornamented bones a very delicate and difficult task. The tubercles on the dorsal part of the post-rostral are elongate toward the posterior. The center of ossification seems to be the dividing line for the change in direction of the tubercles.

That portion of the nasals which is nearest to the dorsal side of the internal nares is ornamented with tubercles which point in a posterior direction. Opposite the internal nares the tubercles are more erect, and ventral to the same point the tubercles have reversed direction and point ventrally. On the lateral margin of the nasals the ornamentation consists of longitudinal ridges parallel to the margin of the bone. The ridges curve around the dorsal and median side of the lateral nares. On the dorsal portion of the nasals the tubercles are longer and more widely spaced.

The ornamentation of the frontals consists entirely of tubercles. They are most heavily concentrated around the center of ossification, close to the lateral edge about midway on the length of the bone. The tubercles anterior to the center of ossification point posterior as if to streamline the pattern; those median and lateral to the center of ossification point away from it. Except over the center of ossification the ornamentation is not as concentrated on the frontals as it is on the post-rostral.

The parietals are not strongly ornamented. There is a low ridge around the lateral and posterior edges of the bone; elsewhere there is a scattering of low tubercles more widely spaced than those of the frontals.

The extrascapular is exposed from the internal surface so nothing can be said of its ornamentation. From a fragmentary

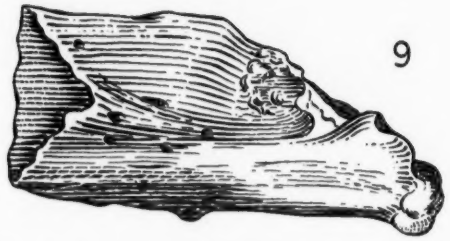

FIG. *9*—*Lawnia taylorensis* Wilson, *gen. et sp. nov.* Enlargement of antero-medial side of right palatoquadrate preserved on B.E.G. no. 30966-401. ×8.

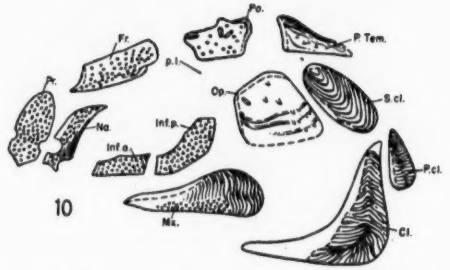

FIG. *10*—Diagrammatic sketch to illustrate ornamentation of dermal bones of the skull of *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×1.

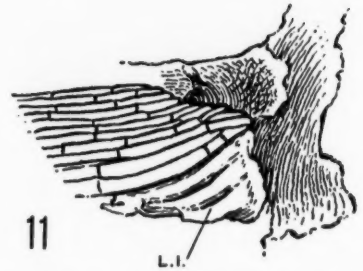

FIG. *11*—B.E.G. no. 30966-404, *Lawnia taylorensis* Wilson, *gen. et sp. nov.* Proximal portion of right pectoral fin. ×4.

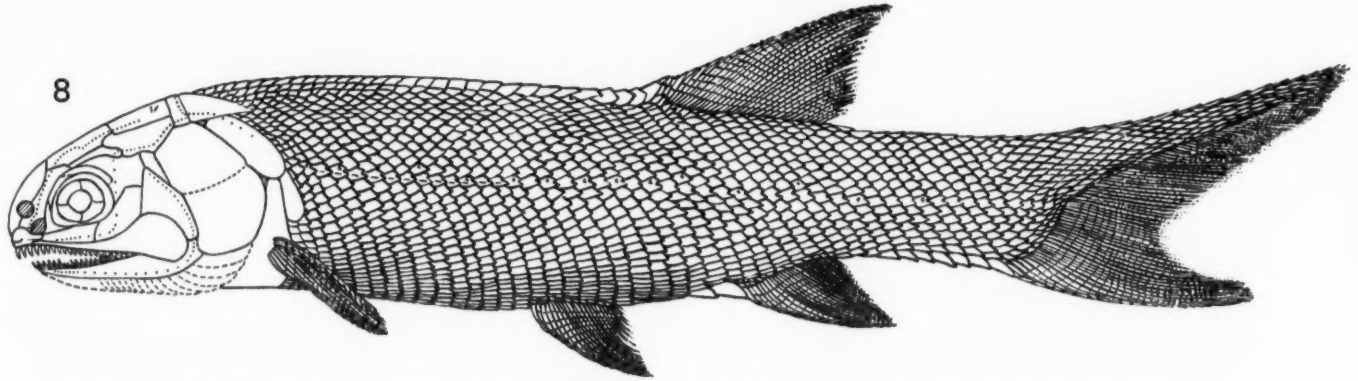

FIG. *8*—Attempted restoration of complete fish. *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×1 circa.

post-temporal exposed on specimen no. 401, it is possible to make out that the posterior and medial edges were surrounded by a prominent ridge and that the more central portion of the bone bore widely scattered tubercles, perhaps only three or four at the most.

The ornamentation of the anterior and posterior infra-orbitals is similar to that on the post-rostral except the tubercles are finer.

The anterior process of the maxillary is thickly covered by ventrally overhanging striated tubercles. Some of these are as large as or larger than the teeth. Near the base of the expanded posterior process of the maxillary the tubercles become more widely separate, and a series of vertically directed ridges appears. At this position they are short and straight, but toward the posterior margin of the bone they become longer and are subparallel to it.

The pre-operculum is exposed from the internal surface only.

The supracleithrum is ornamented by a series of parallel concentric ridges which center slightly dorsal to the center of the bone. The post-cleithrum is ornamented in a similar way, but the center of the ridges is ventral to the center of the bone. The cleithrum bears an ornamentation of parallel ridges which are not parallel to the margin of the bone but intersect it at varying angles.

Dentition.—The dentition is weaker than that found in *Brachydegma* (Dunkle, 1939, fig. 1). The teeth form slender cylinders capped by sharp tips of enamel. The caps are sometimes recurved anteriorly or posteriorly. The teeth in the anterior portion of the jaws are longer than those in the posterior part. The teeth as illustrated in figure 8 are slightly enlarged.

Sensory canals.—The course of the sensory canals (figs. 6 and 8) follows the typical paleoniscoid pattern. With the exception of the pit lines on the parietals and the ethmoidal commissure, all courses of the sensory canals were determined from the ventral surface of the bones or where fractures had exposed the filling of the canal itself. Because of the heavy ornamentation on the external surface of the skull roofing bones, it proved to be impossible to determine the pore openings. There is no marked external groove to show the course of the canals except on the rostrals. This condition is similar to that found in *Glaucolepis* (Nielsen, 1942).

Specimen no. 9 (fig. 4) exhibits a well-preserved left rostral. The ornamentation was very carefully cleaned, and in so doing the course of the ethmoidal commissure was discovered. The sensory canal here lies on the external surface of the bone but beneath the level of the ornamentation tubercles. There is no indication of a ridge on the internal surface of the rostral exposed on specimen no. 180. The course of the canals on the rostral will be apparent from figure 6. The antorbital canal enters the dorsomedian edge of the rostral and continues to within 1 mm. of the ethmoidal commissure. The infra-orbital canal enters deep in the bone on the lateromedial side, proceeds to the surface in a very short distance and then turns ventrally beneath the end of the supra-orbital canal to end about 1 mm. short of the ethmoidal commissure. The ethmoidal commissure is confined entirely to the anterior face of the rostrals. The sensory canals on the rostral bones are in sharp contrast to those on the other bones because here they are open canals, whereas on the other bones they are enclosed deep within the bone.

The supra-orbital canal continues in a posterior direction from the rostral to the nasal, to the frontal, and to the anterior half of the parietal where it ends beneath the pit lines. This seems to be another instance of a transitional stage between a sensory canal and a pit line. (See discussion in Nielsen, 1942, p. 205.) The posterior and anterior pit lines (fig. 2) are placed at an acute angle to each other. They occur as raised folds with the narrow canal-like opening at the highest part of the fold. No other pit lines were observable, although a careful search was made on the maxillary, preoperculum, and the dentary bones.

Those parts of the courses of the other canals that could be seen were in the normal position. The bend from an anteriorly directed course to a ventrally directed course on the posterior margin of the dermosphenotic is clearly shown in specimen no. 403. Its course ventrally from this point is

lost because of the missing suborbitals, but it is found again on the ventral portion of the posterior infra-orbital on the same specimen.

Only a fragment of the supratemporal commissure was observed on specimen no. 403 so that its full course at this point is unknown. The same is true for the cephalic division of the main lateral line on the post-temporals and the supracleithra. They have been restored with widely spaced dots on figure 8. The pre-opercular canal was observed as a ridge on the internal surface of the pre-operculum on specimen no. 403. That portion between the ventral margin of the pre-operculum and the lower jaw is lost. It can be observed for part of its course on the dentary.

Neural endocranium.—All specimens used for the basis of this paper are laterally compressed in such a way that the neural endocranium has been destroyed.

Paired fins.—Specimens no. 180 and 404 are the only ones on which the pectoral fins are well preserved. The former shows the left fin projecting from beneath the cleithrum; the latter shows the base of the right fin with the right cleithrum removed. In both cases the leading edge with the fulcra is in an anteroventral position as preserved on the blocks. The remaining part of the edge is almost vertical but with a slight trend in a posterior direction. In specimen no. 180 (fig. 5) the cleithrum seems to have been tilted so that its dorsal process has been moved anteriorly. This would perhaps swing the posterior margin of the insertion of the fin dorsally from a horizontal position. Both specimens have been crushed flat during fossilization.

There has been considerable discussion concerning the position of the plane of attachment of the pectoral fin to the body. Watson (1925) held that the paleoniscoid fin was attached horizontally. E. I. White (1939) found that in *Cornuboniscus* the attachment was vertical. Nielsen (1942) came to the conclusion, after a reëxamination of Aldinger's (1937) restoration of *Paleoniscus*, that the orientation of the pectoral fin is nearly vertical in *Pygopterus*, *Boreosomus*, *Acrorhabdus*, and *Tarassius* as well as *Cornuboniscus*. Westoll (1944, p. 83) found that for *Haplolepis* and *Pyritocephalus* "in both pectorals and pelvics the anterior insertion of the fin is very slightly higher than the posterior." Westoll further discusses the mechanical significance of the position of the paired and unpaired fins.

Specimen no. 180 has approximately 15 rays on the pectoral fin. This is perhaps an inaccurate count, and better preserved material may revise the count upward.

Specimen no. 404 shows very clearly the arrangement of the proximal ends of the fin rays (fig. 11). The position on the block is as described above with the leading lepidotrich anteroventral to the others. The other bones in this portion of the specimen are little disturbed nor are the scales disturbed, but in the process of flattening the specimen, the posterior edge of the fin may have been elevated.

The first lepidotrich is large and probably compound. It has a broad flattened base which appears to be triangular in shape. From the distal surface of the base two grooves run parallel to the fin rays. These grooves perhaps represent the position of fusion of three fin rays into an anterior cutwater. The first groove marks off the shortest lepidotrich-like element which is also the narrowest. The second groove marks off a somewhat longer and broader lepidotrich-like element. The structure gives the appearance of three triangles stacked against one another with each succeeding one larger. The proximal ends of the fused lepidotrichia are expanded into a rounded blunt base. On specimen no. 404 the base lies in contact with a plate of bone whose edges are broken and lost. This is undoubtedly all that is left of the primary shoulder girdle. The dorsal (as oriented on the specimen) edge of the remnant of the primary shoulder girdle dips beneath the last lepidotrich and continues in a smooth sheet of bone on the proximal side of the bases of the lepidotrichia as far as could be excavated with a needle. This sheet of bone is in the proper position of the mesocoracoid arch. To have determined this certainly by complete excavation would have destroyed the bases of attachment of the lepidotrichia. This could not be done because there is only one specimen in which they are preserved.

The endoskeleton of the pelvic girdle has not been found in any of the specimens.

The number of fin rays of the pelvic fin is approximately fifteen. The fin rays are jointed throughout their length and undivided, or possibly divided only at their most distal ends.

Squamation.—The preservation of the squamation of entire specimens is relatively poor. The soft clay splits so as to cause considerable damage and makes counting of the scale rows difficult. In all specimens the figures are within one or two rows of being correct. The method of notation followed by Westoll (1914) is the one used below.

Specimen No.				
9		35		
244		33		21
	18	26	47	
305		31		20
	17	26	46	
400		33		21
	17	25	45	

The writer is indebted to Dr. David H. Dunkle, Assistant Curator in Vertebrate Paleontology of the U. S. National Museum, who kindly volunteered to make thin sections of the scales. Dr. Dunkle not only made the thin sections but also furnished the author with the drawings (figs. 12–15) and a report of his diagnosis of the salient features shown by the thin sections. The writer is also indebted to Mr. William D. Crockett, staff artist of the National Museum. Dr. Dunkle (personal communication) reports:

> In terms of Aldinger's studies, the pertinent characteristics of these scales would appear to be as follows: the canal plexus of the cosmine layer is composed of concentric and radial tubules. The concentric canals show few, if any, radial cross connections and alone bear the tree-like dentinal structures. The radial tubes penetrate obliquely the bony foot-plate of the scales, sending feeder branches upward into the concentric canals. Except centrally, therefore, the radial tubes lie at much deeper levels than the concentric ones. The radials enter the scale along the dorsal, posterior, and ventral margins with a maximum concentration postero-ventrally. Neither radial nor concentric canals were observed in the anterior portion of the scale. No ascending branches of the cosmine canal plexus were seen to penetrate the external enamel layer, but this point should be checked further.
>
> Not shown in the accompanying diagrams is the distribution of the "fibers of Sharpey." If the four corners of the scale are connected with diagonals the fibers, as viewed from a frontal plane, appear concentrated in the dorsal and ventral triangular quadrants. In the anterior quadrant only a few of the fibers are to be seen radiating near the center and none were observed posteriorly.
>
> To my knowledge, no scales have ever been described in exactly these terms. Any definitive identifications of fish based on scale histology are premature. However, the arrangement of the radial and concentric canals, entire enamel cap, etc., would seem to limit consideration of relationship to three of Aldinger's families: Elonichthyidae, Paleoniscidae, and Dicellopygidae—the latter in the event that *Brachydegma* is correctly referred.

RELATIONSHIPS

The latest and perhaps most successful attempt to divide the family Paleoniscidae, s.l., is that of Aldinger (1937) who used histological characters of the scales as his basis of subdivision. Since all paleoniscoid scales have not been so studied, it is too early to tell if his method is successful. Present-day groupings of paleoniscoids are based on a summation of characters, with the determination of the relative weight of the respective characters in the hands of the individual author. There has been little uniformity in the assignment of values to these characters.

For many years practically all Permian paleoniscoids were assigned to either of the two genera *Paleoniscus* or *Amblypterus*. Most of the species were based on characters that now prove to have been accidents of preservation. The taxonomic condition of the paleoniscoids had grown so confusing that Traquair (1877) asked the questions "What is an *Amblypterus?* What is a *Paleoniscus?* How do we distinguish them?" He then set out to define both genera and to separate out from them previously referred species and to erect new genera.

Since 1877 *Paleoniscus* has received considerable attention by various authors, but little, if anything, has been added to the knowledge of *Amblypterus*. Traquair's (1877) definition still stands as the most authoritative diagnosis of *Amblypterus*.

The description of *Lawnia* seems to indi-

cate that this genus belongs near or in either of the families Paleoniscidae or Amblypteridae or to a family which exhibits elonichthid scale structure and elonichthid skull pattern.

Concerning the family Paleoniscidae of Aldinger, Nielsen (1942, p. 276) writes as follows:

> Common to the four genera are the following characters: I) the *Elonichthys*-like shape of the frontal and the supratemporo-intertemporal; II) the two pairs of extrascapulars; III) the presence of two series of supraorbitals, a lateral and a medial, which are either separate or present as components in compound bones; IV) the very oblique suspensorium; V) the large operculum; VI) the rather faint ornament on the dermal bones of the head; VII) the horizontal pectoral fin; VIII) the small scales.

Of the preceding points *Lawnia* agrees with I, III, VII (?), and VIII. That is somewhat less than halfway agreement, giving equal weight to all eight of the characters.

Comparison, point for point, with Traquair's (1877) description of *Amblypterus* demonstrates that *Lawnia* agrees with *Amblypterus* with the single exception of the body shape. It can be demonstrated, however, that there is little hesitancy on the part of authors to include forms of slender fusiform shape within the same genus as forms with moderately deep bodies, e.g., *Elonichythys serratus* and *E. pulcherrimus* (Moy-Thomas and Dyne, 1938). Rather than assign the forms herein described to *Amblypterus*, a form that has not been studied in detail by modern methods, the writer has felt that the proposal of a new genus is thoroughly justified. A revision of *Amblypterus* would necessitate travel to several European centers, which is practically impossible today.

It would seem, therefore, that *Lawnia* agrees more closely with *Amblypterus;* and until detailed studies of the European forms prove this contention one way or another, this author tentatively assigns *Lawnia* to the family Amblypteridae.

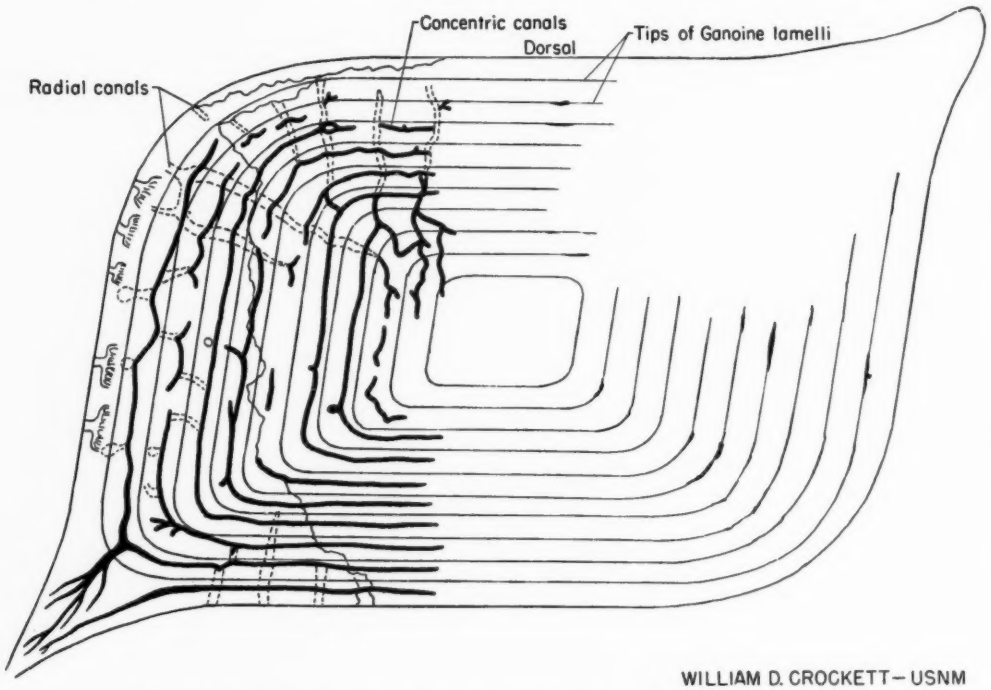

FIG. *12*—Horizontal section through mid-lateral scale of *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×35.

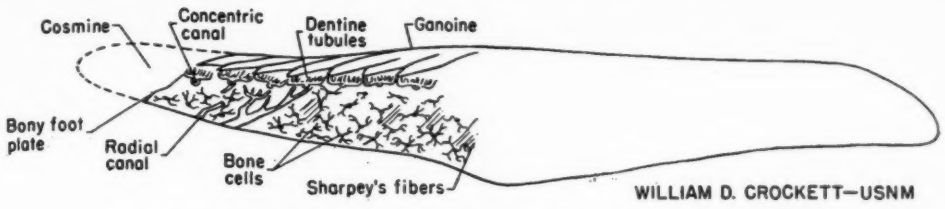

FIG. *13*—Antero-posterior cross section through mid-lateral scale of *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×45.

FIG. *14*—Dorso-ventral cross section through mid-lateral scale of *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×55.

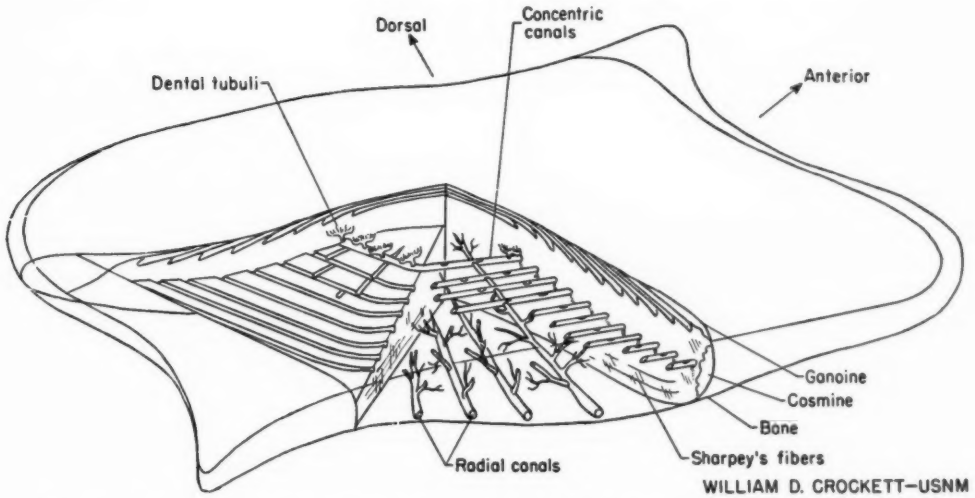

FIG. *15*—Diagrammatic restoration to show relationship of structures in planes of section of mid-lateral scale of *Lawnia taylorensis* Wilson, *gen. et sp. nov.* ×35.

LIST OF ABBREVIATIONS USED IN FIGURES

Ant.	Antorbital
A.op.	Antoperculum
Br.	Branchiostegal rays
Cl.	Cleithrum
D.	Dentary
D.sph.	Dermosphenotic
e.c.	Ethmoid commissure
E.sc.	Extrascapular
Fr.	Frontal
Hy.	Hyomandibular
Hyb.	Hyal element
Inf.a.	Infra-orbital, anterior
Inf.p.	Infra-orbital, posterior
F.l.	Fused first lepidotrich of pectoral fin
Mx.	Maxillary
N_1, N_2	First and second external nares
Na.	Nasal
Op.	Operculum
Pa.	Parietal
Pal.	Palatine
P.cl.	Post-cleithrum
p.l.	Pit line
P.op.	Pre-operculum
Pq.	Palatoquadrate
Pr.	Post-rostral
Psph.	Parasphenoid
Pt.	Pterygoid
P.tem.	Post-temporal
Pv.	Prevomer
R.	Rostral
S.	Supra-orbital
S.cl.	Supracleithrum
Sclo.	Sclerotic plates
S.o.	Suborbital
S.o.c.	Supra-orbital canal
S.op.	Suboperculum
St.-it.	Supratemporo-intertemporal

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ONTOGENY AND SEXUAL DIMORPHISM IN *CYTHERELLA BULLATA*

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ABSTRACT—There is disagreement among workers as to the significance of ontogenetic studies for ostracods, particularly those studies concerned with growth. Nine growth stages are found for the Cretaceous *Cytherella bullata* and the Pennsylvanian *Cavellina jejuna*. Growth per stage for each of three differently aged species can be expressed well by a constant percentage of about 19 so that Brooks' law applies except to the male of *Cytherella*. Relative size of the molts is nearly constant for each species. Molt stage morphology of *Cytherella* more nearly parallels that of *Cavellina*, rather than predicting the adult morphology of the ancestral cavellinid. The developmental histories of ostracods should be of value for determining phylogeny and therefore of increasing use in taxonomy.

INTRODUCTION

THE present study was suggested two years ago when I noted that two species of the Carboniferous ostracod *Cavellina*, belonging to the family Cytherellidae, were characterized by very similar growth relationships. Moreover, the growth law as stated in Brooks' law applied quite well to both species. When length-height measurements of a few hundred specimens were plotted on coordinate paper, these particular cavellinids did not fall into separate groups according to sex. Yet it was known that marked sexual differences in length and height are present in some species of post-Paleozoic *Cytherella*, a genus so similar to *Cavellina* that species of cavellinids were once placed with *Cytherella*.

This study was undertaken to further determine the indicated value of ontogenetic studies in fossil ostracods, to test Brooks' law and to determine how it might be modified in fossil species with pronounced sexual dimorphism. Moreover, if persistent growth patterns could be shown to apply over a considerable length of geologic time for this group, further use of methods used herein would be indicated for other ostracods.

Cretaceous cytherellids may be quite dimorphic, and one such species, *Cytherella bullata*, is primarily considered. Specimens came from the Prairie Bluff chalk formation of the Upper Cretaceous. The sample is a blue-gray sandy chalk taken from 6 feet below the contact of the Clayton sand of the overlying Midway, on Mississippi State Route 6, eastern half of Section 33, T. 9 S., R. 3 E., Pontotoc County, Mississippi.

I wish to make acknowledgment to Dr. James W. Ward who kindly consented to criticize the manuscript.

PREVIOUS WORK

The growth of both Recent and fossil ostracods is known to be discontinuous as is characteristic of most other arthropods. Periodically the old shell is discarded and a new one of different size and shape is secreted, resulting in a series of stages or instars. In fossil species, young molts often are found in greater numbers than are adults.

These facts were recognized even for fossil forms by a few investigators at least a hundred years ago. Molting details for many modern groups have long been worked out, but it has been only in recent years that ontogenetic studies in fossil species have received impetus. Much of the pertinent literature has been mentioned by Sohn (1950) and Spjeldnaes (1951). Another study recently completed is my (Shaver, 1951) dissertation in which ontogenetic details are given for nine fossil and one Recent species of the suborders Platycopa and Podocopa. Kesling (1951) has made an outstanding contribution to the knowledge of molt stage morphology in modern freshwater ostracods. These workers have observed that disregarding of the molt series

has often resulted in incorrect classification and have indicated several other applications of ontogenetic studies.

Several workers have tested the applicability of Brooks' law and have arrived at conclusions of some variance. Fowler (1909, p. 324) first stated the law as applied to ostracods as follows: "During early growth, each stage increases at each molt by a fixed percentage of its length, which is approximately constant for the species and sex." Stated as a formula, the law becomes:

$$L_{(n+1)} = L(k+1)$$

where L_n is the length of any stage and k is the constant percentage for the species and sex.

Skogsberg (1920) tested the law for several Recent species of the families Cypridinidae and Halocypridae. Some of his calculated growth factors are: 1.22, 1.21, 1.23, 1.24, and 1.50. As realized by Fowler himself, Skogsberg believed the law should be applied with caution but that it seemed to be very useful as it now stands.

While Przibram's (1931) growth factor of 1.26 for all Arthropoda does not apply to many species of ostracods, it is probably very close to the average of growth factors so far computed.

Sohn (p. 431, 432) observed that neither Przibram's growth factor nor Brooks' law applied in the light of observed data. Spjeldnaes (p. 746) implied that at least part of the reason for this conclusion lies in insufficient data. Reliability of any calculated growth factor is a function of the degree of variation in the species and the number of units entering into its calculation. Variation in ostracods apparently differs with the species and age of the individuals (Elofson, 1941, p. 378; Shaver, p. 128, table 34). Analysis of variation in several fossil species convinces me that lack of sufficient data and therefore lack of understanding of the particular variation at hand, is a principal cause for past invalidation of Brooks' law for fossil ostracods.

Kesling measured 500 valves obtained from a laboratory culture of *Cypridopsis vidua* and concluded (p. 102) that the differences between observed and computed lengths were too great in the last three instars for Brooks' law to be of value for this freshwater ostracod.

Spjeldnaes (p. 746) agreed with Skogsberg that Brooks' law can be accepted in general but with reservations, and stated his observations, while neither proving nor disproving, were favorable to Przibram's conclusions. Spjeldnaes made another significant observation—he believed that the nature of development in fossil ostracods is of value for determination of phylogeny and so used it.

In my previous study, ontogeny was discussed from several standpoints—among them, growth and sexual dimorphism. In the study of growth it was shown that Brooks' law as originally stated applied well to some species and less well to others. Usually it could be relied upon to connect larval forms with the adult and therefore to determine the stage represented by a single specimen. Although in some species constant growth factors were not obtained for a developmental series, the average growth factor appeared rather constant for the genus (p. 78, table 4). Moreover, size relationships of one instar to others appeared to be diagnostic of the genus (p. 75, table 3). Therein seems to lie the greatest value of such studies to taxonomy—in the nature of development and not necessarily in the morphological prediction of an ancestor. However, attempts to use ontogeny in fossil ostracods in the latter manner have been made. As for sexual dimorphism, it was shown that its presence could be detected when other methods failed if a single series of young led up to two morphologically differentiated groups of adults.

The presence of sexual dimorphism is well established in the Cytherellidae. Van Veen (1928) was the first to demonstrate it in fossil *Cytherella*, and Alexander (1932) later figured males and females for several Cretaceous species from Texas. Reported male and female size relationships are not constant in this genus. In some species, sexes are nearly equal; in others, females are larger. Apparently, males are not always present in a sample and may be fewer in number if present. The feature which most characteristically differentiates the sexes is the greater posterior obesity for the female

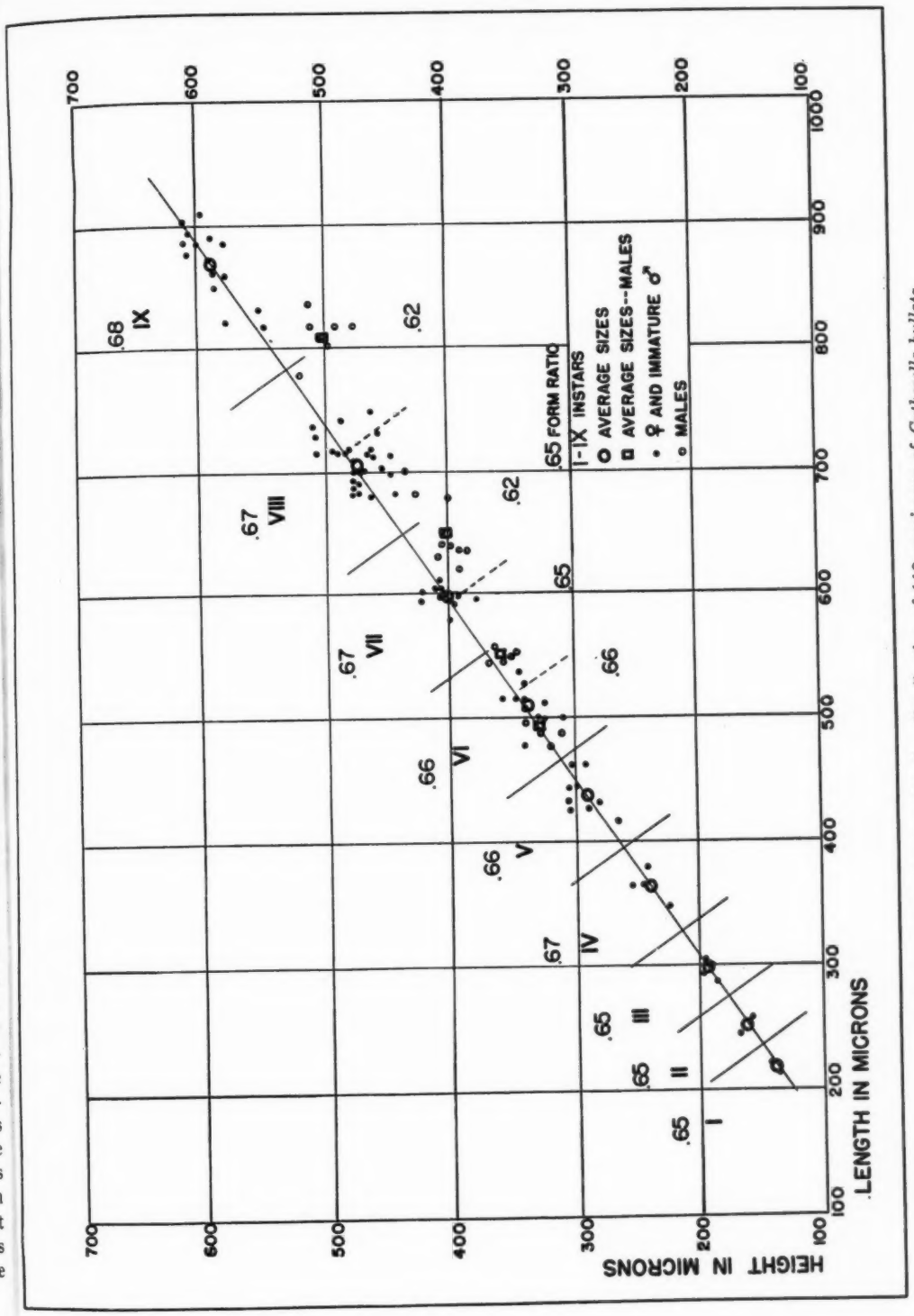

FIG. 1—Graph showing the size distribution of 110 specimens of *Cytherella bullata*.

in dorsal view. Coryell (1928, p. 89) established the Carboniferous genus *Cavellina*, and later, Kellett (1935, p. 145), although realizing it to be a female cytherellid, recommended retaining the name and transferring Carboniferous male species of *Cytherella* to *Cavellina*.

GROWTH RELATIONSHIPS

Figure 1 shows the length-height measurements of 110 specimens of *Cytherella bullata*. The points fall into distinct groups in the smaller sizes, but the pattern becomes more complex in the larger ones. From the sixth group on, two patterns diverge from one. Figure 2, drawings 1, 10, 14, and 22, shows that the larger individuals, belonging to the groups which carry on the straight line trend established in the smaller sizes, are females while the opposed group are males. Differentiation could not be determined in the smaller sizes. Each distinct group, with proper sexual considerations, represents a different instar or stage during development and accordingly are numbered I through IX from youngest to oldest. It is believed that nine instars represent the entire developmental series for the Cytherellidae since nine stages have also been found for Paleozoic *Cavellina* (Figure 3). Relative numbers for each stage are representative of the numbers of carapaces preserved in the sample only in that late-middle instar specimens are most numerous and early specimens less numerous than the adults. If preservation were not a factor, numbers per instar should decrease with increased size.

The growth trend as shown on coordinate paper is nearly a straight line for the female series while that for males is not. The straight line, combined with an increasing absolute interval between instars, indicates that growth accomplished at each molting can be expressed better by a constant percentage, k, rather than by an arithmetic amount. This fundamental principle has not always been a consideration for separating stages of fossil molt series in which natural divisions are not readily apparent.

Figure 3 shows similar relationships for the developmental series of Paleozoic *Cavellina jejuna*. As indicated in the size distribution of several males and females in the ninth instar, sexual differentiation is not demonstrated by this length-height series. However, if posterior thickness were considered, no doubt sexual differences would be demonstrated for one, two, or three earlier instars. Appearance of sex characters as early as the sixth instar gains some support from Müller (1894) and Claus (1872) who reported the appearance of genital organs for the seventh stage in modern ostracods.

Table 1 shows the percentages of total length attained each instar for three differently aged species of Cytherellidae. A remarkable similarity in development for all three species is present. Only in instar 8 is any departure made from the "normal."

TABLE 1.—PERCENTAGES OF TOTAL LENGTH ATTAINED EACH INSTAR

Species	Instar								
	1	2	3	4	5	6	7	8	9
Cytherella bullata[1] F	25	29	34	42	51	59	69	82	100
Cytherella bullata[1] M						60	68	80	100
Cavellina jejuna[2]	24	29	34	40	50	59	71	87	100
Cavellina cavellinoides[3]	24	29	34	41	48	57	69	86	100

F = females.
M = males.

[1] *Cytherella bullata* Alexander, 1932, Jour. Paleontology, vol. 6, p. 101. Prairie Bluff, Cretaceous, Pontotoc County, Mississippi.

[2] *Cavellina jejuna* Coryell and Sample, 1932, Am. Midland Naturalist, vol. 13, p. 274, pl. 26, fig. 16. Exline shale, Pennsylvanian, Peoria County, Illinois (data from Shaver, 1951).

[3] *Cavellina cavellinoides* (Bradfield), 1935, Bull. Am. Paleontology, vol. 22, p. 124, pl. 11, figs. 3a, b. Lonsdale zone, Pennsylvanian, Vermillion County, Illinois (data from Shaver, 1951).

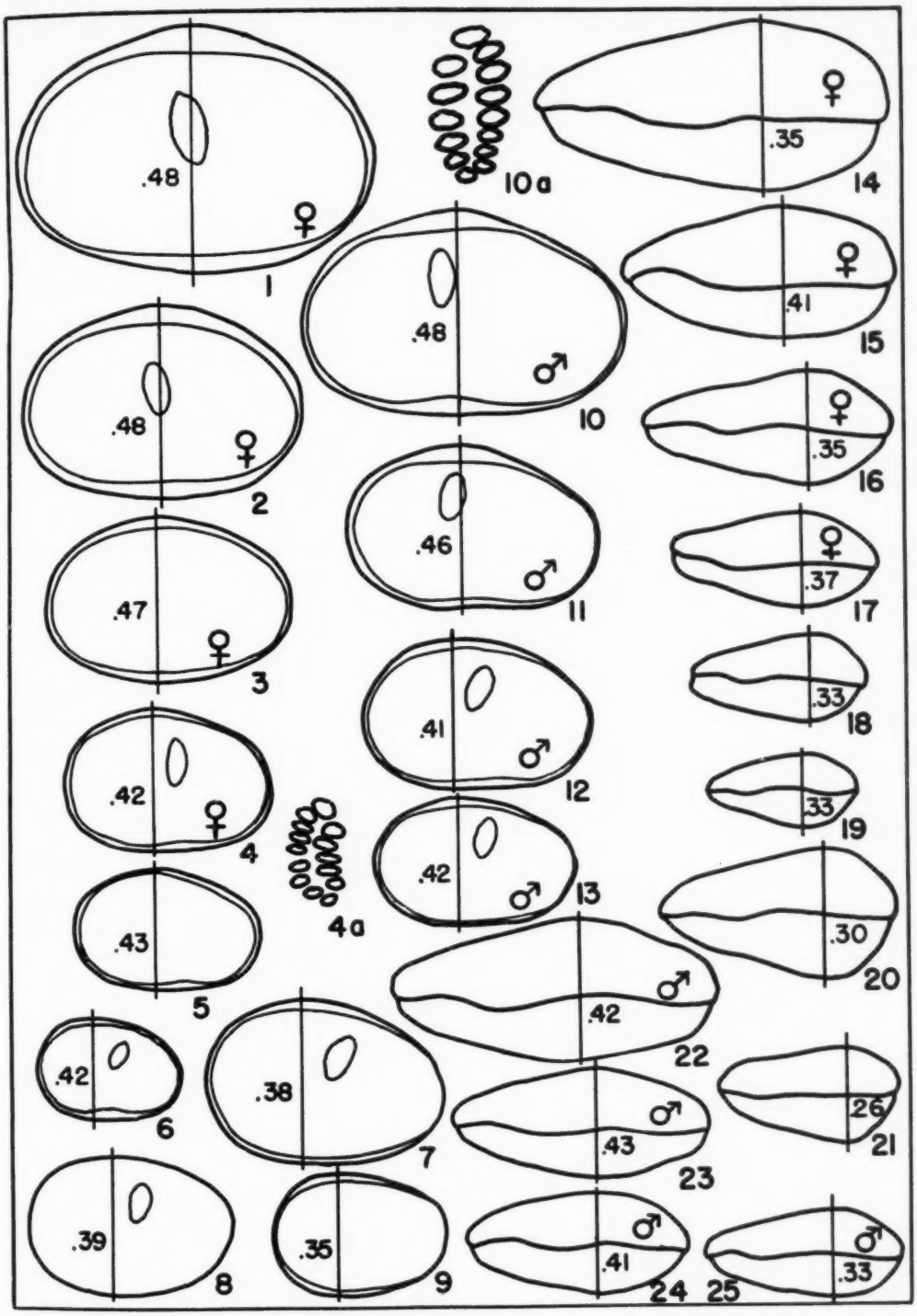

FIG. *2—1–4*, Left valve views of females, instars 9–6 respectively. *4a*, Adductor muscle scar, female, instar 6. *5–7*, Left valve views, instars 5–3. *8*, Interior right valve view, instar 2. *9*, left valve view, instar 1. *10a*, Adductor muscle scar, male, instar 9. *10–13*, Left valve views of males, instars 9–6. *14–17*, Dorsal views of females, instars 9–6. *18–21*, Dorsal views, instars 5, 4, 3 and 1. *22–25*, Dorsal views of males, instars 9–6.
All drawings ×60 except *4a* and *10a* which are ×196, and *7*, *8*, *9*, *20*, and *21* which are ×120

Figures for the first three stages are nearly identical, while any slight differences shown are for later stages. Ecological factors during growth probably bear on this condition. Of course, the male *Cytherella* series if projected back would depart from the mean, but previously it was indicated that the male is least consistent in an adult population and therefore, apart from its "abnormality," is considered least diagnostic of *Cytherella*.

Table 2 shows average lengths and increments in microns and percentage increases each instar for three species of Cytherellidae. The average percentage increases or

TABLE 2.—AVERAGE LENGTHS, INCREMENTS AND PERCENTAGE INCREASES EACH INSTAR

Species		Instar									Ave.
		1	2	3	4	5	6	7	8	9	
Cytherella bullata (females)	L	216	250	294	364	439	508	597	707	867	
	I		34	44	70	75	69	89	110	160	
	%		15.7	17.7	23.7	20.6	15.9	17.4	18.5	22.6	19.0
Cytherella bullata (males)	L					439	490	549	649	809	
	I						51	59	100	160	
	%						11.6	12.2	18.3	24.6	16.7
Cavellina jejuna (males and females)	L	267	314	375	443	548	646	779	953	1098	
	I		47	61	68	105	98	133	174	145	
	%		18	19	18	24	18	21	22	15	20
Cavellina cavellinoides (males and females)	L	254	297	352	422	500	592	720	892	1038	
	I		43	55	70	78	92	128	172	146	
	%		17	18	22	18	18	22	24	16	19

corresponding growth factors of 1.19, 1.20 and 1.19 are very close considering the amount of time separating the species. Since differences in length were not apparent for sexual dimorphants of *Cavellina*, figures are for both sexes. Sexual dimorphism is so pronounced in *Cytherella bullata* however, that males are considered separately, and the average percentage increase of 16.7 for them is not representative of any one stage. Brooks' law, then, certainly does not apply to males of this particular species.

Although percentage increases vary somewhat from the mean throughout each entire series, this does not invalidate Brooks' law. A better test is made by comparing observed lengths with lengths computed by using mean growth factors. Comparisons are made for two species in Table 3. Computed lengths for both species agree very closely with observed lengths. Greatest error for a stage is three and one-half percent for *Cytherella* and four percent for *Cavellina*, but most errors are considerably less and negligible. Thus, the computed growth factor can be used quite well to connect larval forms with the adult. It is further suggested that a growth factor of about 1.20 might be characteristic for most Cytherellidae and could be used to clarify the molting history of species not represented by numerous young individuals.

It has been noted that three species have nearly identical average growth factors and that Brooks' law applies well to the two species tested. Therefore, the method of expressing similar developments by determining percentages of total length attained each instar is only another way to express the two conditions just stated. However, this method could be effective even though Brooks' law were invalid.

Salient parts of the foregoing discussion and data are summarized:

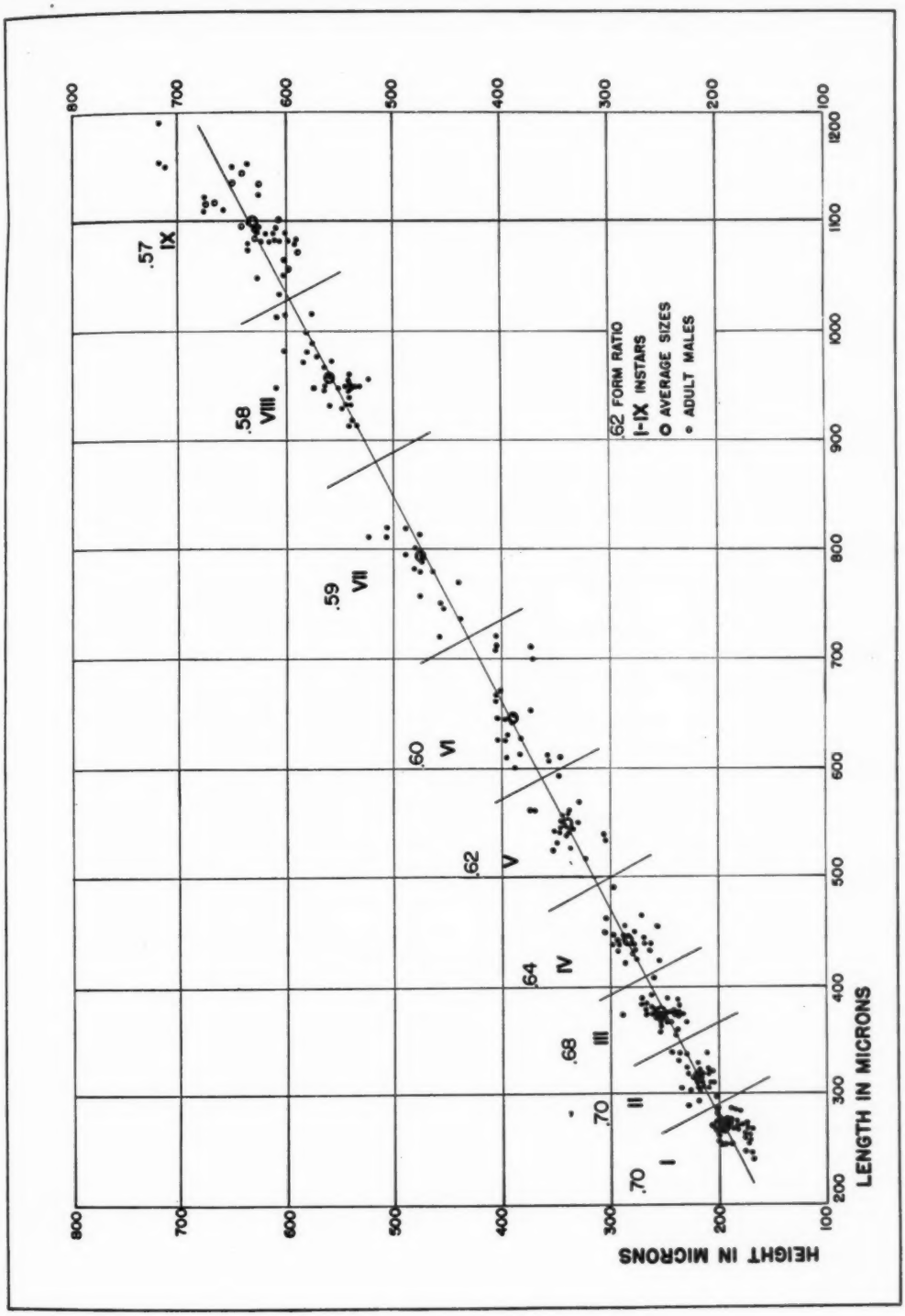

FIG. 3—Graph showing the size distribution of approximately 260 specimens of *Cavellina jejuna*.

1. Nine growth stages are characteristic for the Cytherellidae.
2. Three non-contemporaneous species exhibit very similar size relationships among their molt stages. The smallest molt has a length of about 25% that of the female adult.
3. Three species have nearly identical average growth factors. In addition, growth factors for individual stages are close enough to the mean that Brooks' law applies.
4. While in two species the male behaved in a manner predictable by Brooks' law, it did not for the third. The male dimorphants may then modify the conditions stated in 2 and 3.

TABLE 3.—BROOKS' LAW

Instar	*Cytherella bullata*, $k=19$		*Cavellina jejuna*, $k=20$	
	Observed L	Computed L	Observed L	Computed L
	microns	microns	microns	microns
1	216	216	267	267
2	250	257	314	320
3	294	306	375	384
4	364	364	443	461
5	439	433	548	544
6	508	515	646	652
7	596	613	779	783
8	707	729	953	940
9	867	868	1098	1127

Since only prosaic Cytherellidae are considered here, specialized groups even within this family may depart from the indicated patterns. However, similar growth characteristics for related but time- and geographically-separated species of Cytherellidae suggest they are worthy of further study and evaluation for other groups of ostracods. Although ecological factors may affect growth patterns more than inherited qualities in some instances, such factors may also effect a proportional departure in morphological features and thereby not decrease the relative value of growth studies. I therefore suggest, as indicated so many years ago from the studies of Fowler and Skogsberg, but still neglected, that growth studies of fossil ostracods reveal characteristics of value in taxonomy and ones which can help paleontologists take a step away from the artificiality of much of the present ostracodal systematics. Certainly a statement of the developmental characteristics at a certain level should be as informative as: "Minute, mostly reniform or elongate-ovate, corneo-calcareous shells with thin, more or less unequal valves, one overlapping the other either ventrally or dorsally or both," a family description now in use which is too broad to furnish even a morphological basis upon which phylogeny can be expressed. The trend in classification seems to be toward greater emphasis of phylogeny, and such studies should become increasingly useful.

MOLT STAGE MORPHOLOGY FOR *CYTHERELLA BULLATA*

Average sizes for each stage as expressed by length and height and computed from specimens represented in Figure 1, are shown in Table 4. Adult male length is 93% of that of the female, while height is 85%. Form ratios, determined by dividing heights by lengths, are shown in Figure 1. They indicate a slight progressive "shortening" of the carapace for the female, but a "lengthening" for the male. Figure 3 shows that carapaces of both sexes in *Cavellina jejuna* become relatively longer with age.

For some time it has been known for modern ostracods that the posterior portion of the carapace in lateral view "fills up" with age. This is believed to correspond to

TABLE 4.—AVERAGE LENGTHS AND HEIGHTS FOR *Cytherella bullata*

Instar	Females		Males	
	Length	Height	Length	Height
	microns	microns	microns	microns
1	216	139		
2	250	163		
3	294	192		
4	364	243		
5	439	291		
6	508	337	490	328
7	597	400	549	359
8	707	473	649	403
9	867	588	809	500

posterior addition of appendages and sex organs with age. This condition is present in fossil *Cytherella* as shown in Figure 2. A feature dependent upon the filling up of the posterior is the "moving" of the line of greatest height posteriorly with age. It is well forward in instar 1 but is centrally located in the adult. A numerical expression of this development is obtained by dividing distance of the line of maximum height from the anterior margin by length. In a sense, bluntness of the anterior portion of the carapace is measured (Kesling, p. 104). Ratios in Figure 2 indicate a general decrease in anterior bluntness with age for both sexes. The reverse situation applies in dorsal aspect. Not only are the young relatively thicker in the posterior, but the line of greatest thickness "moves" anteriorly with age. The adult female reverses this trend. Ratios in Figure 2 indicate that posterior bluntness in dorsal view decreases with age. Values were obtained by dividing distance of the line of maximum thickness from the posterior margin by length.

Relative thickness generally decreases with age, with, however, the adult female again reversing the trend. Ratios, thickness divided by length, for single carapaces representing instars 1 and 3 through 9 in the female series are .51, .52, .46, .46, .45, .45, .46 and .47. Figures for males in instars 6 through 9 are .44, .43, .41 and .40.

Considering three dimensions, the cytherellid male became differentiated in general outline by a relative increase in length and decrease in height and thickness, while the particular cavellinid male under consideration became differentiated only by changes in thickness.

In some fossil ostracods, the posterior extremity becomes higher with age. This is not true for *Cytherella bullata* since stability of this extremity is present if the established practice of placing the venter in as nearly a horizontal position as possible, is maintained.

The adductor muscle scar during development maintains the same configuration (14 spots in an elliptical area) at least well down toward the early stages (figure 2, drawings 4a and 10a). It "moves" from a posterior position in youth to a central to anterior one in maturity, which feature is also dependent upon posterior lengthening with age. The axial inclination "pivots" from a backward inclination to a forward one with increased size. *Cytherella* and *Cavellina* differ considerably in muscle scar pattern, the latter having three to four times as many spots. The young of *Cytherella* do not take on the configuration of their ancestral stock as represented by *Cavellina*.

The position of greatest stability in valve overlap is in the dorsal and ventral positions. Overlap at the extremities is almost absent in the early stages but is emphasized with age. Dorsal and ventral overlap is conspicuous in all stages if relative size is considered.

Morphology of cavellinid molt stages is very similar although the two genera are so far apart in time. Cytherellid young do not resemble the adult *Cavellina*—rather they are quite similar to the young of *Cavellina*. This, combined with similar growth relationships, suggests major anatomical features were much the same for the two represented times. Thus I believe that degrees of similarity or dissimilarity of ontogenetic series among the Ostracoda are of greater value for determining relationships than are attempts to relate morphological features of a given set of young to a geologically older adult. It is difficult to see how shells of newly hatched young with three pairs of appendages can resemble an adult shell (classifiable as an ostracod) which enclosed seven pairs of appendages and fully developed sex organs. Such an observation may seem naive, but ostracodal literature contains references apparently stemming from blind adherence to the principle "ontogeny recapitulates phylogeny."

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MANUSCRIPT RECEIVED MAY 17, 1952

NOTICES

INVERTEBRATE PALEONTOLOGY—1953

Special conference sponsored by the Paleontological Society for the 1953 meetings in Toronto

Program Committee: N. D. Newell, J. W. Durham, B. Kummel (Chairman)

Synthesis of knowledge of fossil invertebrates is a primary goal of many paleontologists in connection with preparation of the projected TREATISE on Invertebrate Paleontology. Modern inventories by specialists provide the means for a new appraisal of fossil invertebrates. It is now feasible and timely to seek understanding and direction by focusing attention on basic principles arrived at through familiarity with the major animal groups. With this aim in mind, several persons have been invited to speak briefly on subjects in which they have demonstrated special competence.

Two sessions of the 1953 meeting of The Paleontological Society will be devoted to the broader aspects of evolution and systematics of the invertebrates. In the first session several major groups will be discussed by specialists who will briefly outline modern thought relative to genera' principles as applied to each group. Evolutionary patterns and principles of classification will be stressed. Time will not suffice for discussion of taxonomic and morphologic details. These talks will aim to summarize in perspective for the non-specialists the present status of the separate groups.

The second session will be devoted to the broad interrelationships in time of the invertebrate phyla and will be led by three paleontologists and one zoologist.

NEGATIVES OF PALEONTOLOGICAL PAPERS AVAILABLE AT THE PALEONTOLOGICAL RESEARCH INSTITUTION

There have accumulated at the Paleontological Research Institution negatives of copies of plates of publications relating to paleontology. These were made for the purpose of obtaining copies of unavailable publications and/or making card catalogues. With the high cost of film and the saving of time in duplicating such negatives it would seem that these negatives might be of service to workers who do not have such publications accessible. A list of the negatives with key reference is available from the Director. Workers may borrow the negatives for a reasonable time at the cost of transportation. Some of the negatives are slightly soiled but they are adequate for card catalogue purposes.

KATHERINE V. W. PALMER, *Director*
Paleontological Research Institution
109 Dearborn Place, Ithaca, N. Y.

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 3, PP. 481–485, MAY 1953

THE SYSTEMATIC POSITION OF ARCHAEOCYATHA (PLEOSPONGES)

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ABSTRACT—The position of the Archaeocyatha is reconsidered, and it is concluded that they should be ranked as a distinct phylum under the sub-kingdom Parazoa.

INTRODUCTION

IN THE past the Archaeocyatha (Pleospongea) have been classed with corals, calcareous and siliceous sponges, Protozoa, and calcareous algae. Billings included them with the Protozoa, but recognized the possibility of an intermediate position between the corals and the sponges. Sir William Dawson considered them to be Foraminifera, whereas Von Toll suggested an affinity with the calcareous algae. Hinde refuted the alleged affinities to the Foraminifera, while Taylor (1910) conclusively showed the lack of any relationship to the algae. In the following years opinions were almost equally divided between those favouring affinity to the Coelenterata and those preferring the Porifera. So Walcott, Taylor, and Raymond were for the calcareous sponge hypothesis, while Bornemann and Hinde leaned towards the corals.

The more recent work of Vologdin, Bedford, and Okulitch brought out a wealth of detail which made it impossible to place the Archaeocyatha with the Coelenterata. The lack of mouth, coelenteron, and mesenteries makes the anatomy of Archaeocyatha incompatible with the most basic structures of the Coelenterata. This very impossibility to reconcile Archaeocyathine structures with those of the corals made Okulitch (1943) place them as a separate class Pleospongea of the phylum Porifera.

Ting, (1937) having seen what he thought were siliceous tetraxon spicules in Sardinian specimens of Archaeocyatha placed the entire group into Silicispongea. He was blindly followed by Simon (1939). Needless to say there is no evidence whatsoever to make us accept their views.

Placing the Archaeocyatha in the Porifera as an independent class, while temporarily convenient, was not entirely satisfactory, as it was realized from the very beginning that there are some very serious differences in the skeletal structures of the Calcispongea and Pleospongea. The matter was finally brought to a head by the participation of both authors of this article in the preparation of the chapter on the Porifera for the forthcoming "Treatise on Invertebrate Paleontology." It became necessary to review and determine the systematic position of the Archaeocyatha. After considerable thought and discussion it was decided that the entire problem can be best solved by placing the Pleospongea in a separate new phylum Archaeocyatha, which together with the phylum Porifera, will constitute the sub-kingdom Parazoa.

For the sake of completeness the entire discussion of possible affinities of the Archaeocyatha to the Coelenterata and the Porifera is here presented. It is hoped that this discussion will make it clear that the Archaeocyatha are neither Coelenterata, nor sponges, and while somewhat closer to the sponges, nevertheless rate a phylum of their own. It is regarded as obvious that neither the size nor the life span of a phylum is of any importance as far as a general scheme of classification is concerned.

BASIC CHARACTERISTICS OF THE ARCHAEOCYATHA

The Archaeocyatha are exclusively Cambrian marine organisms with world-wide distribution. They lived in large numbers on calcareous bottoms, forming "gardens" or carpets of sessile benthos, but lacked the ability to build true topographically prominent bioherms. In the Cambrian epeiric seas they apparently lived some distance from shore, in relatively narrow belts paralleling

the shore-line. Their tolerance to muddy water was low, nor could they successfully defend themselves against encroachment by the algae. In North America and Australia the Archaeocyatha became extinct at the same time as the Olenellidae, that is, at the close of early Cambrian, in Eurasia they may have continued till the end of the Middle Cambrian. No discernible descendants have been recognized in later times. The phylum is therefore a short-lived one. During its short life-span, however, a bewildering array of forms was produced indicative of an almost explosive evolution.

The Archaeocyatha built their skeletons out of calcium carbonate. The skeletons are exceedingly fragile and their fragments sometimes resemble large spicules. The most typical skeletons are goblet or vase-shaped, although irregular, crenulated cone or saucer shapes are also encountered. The skeleton of the simpler types consists of an outer cup or cone and an inner cup fitting inside. The inner cup is supported some distances from the outer cup by a variety of structural elements. In the most common types, such as *Ajacicyathus* these supports are in the form of vertical, radial plates, called septa or parieties. The outer cup is a conical structure perforated by numerous and usually very fine pores. It is referred to as the outer wall, and its shape may vary quite considerably. It may be an acutely tapering cone, an almost cylindrical cup, or a more widely open cone, in the most extreme cases resembling a flat saucer rather than a cup. The cross-section may be almost perfectly circular, but more often is irregular, varying from an ellipse to an irregularly crenulated expansion. Besides these irregularities of the outline and the variations in the apical angle, the cup may also be crenulated in the transverse direction resulting in a corrugated appearance. In some genera the cup is also fluted longitudinally, the grooves usually corresponding to the locus of attachment of a paries to the outer wall.

The outer wall may be connected to the inner by vertical plates—parieties, horizontal or inclined bars or rods, horizontal or curved plates—tabulae, by complex curved plates—taeniae, by even more complex vesicular tissue or by cellular or tubular structures. These may be further complicated by dissepiments and synapticulae, the former being small horizontal or curved plates extending from pariety to pariety, and the latter tangential rods connecting neighboring parieties. Most of these structures are also porous. The size of the pores varies from very fine to pores of such size that only a very slender net-work is left of the pariety or tabula.

The inner wall is usually concentric with the outer wall and so forms a cup or cone similar to the outer cup. In some cases this inner cone may be open at the lower end. The inner wall is perforated by numerous pores, and commonly the number and size of pores is such that it is reduced to a network of anastomosing and fused rods and bars. The inner wall encloses the central cavity which in all probability has been free of living tissue, though probably lined by it, and was completely open upward. In some genera the lower portion of the cavity may be filled with irregular vesicular tissue. Minor structures may also project a short distance from the inner wall into the central cavity.

The space between the inner and outer wall is called the intervallum, which is divided into intersepts by the parieties. Its width tends to remain constant throughout most of the growth of the individual. Okulitch (1946) has shown that all the skeletal surfaces of the intervallum are covered during life by a layer of living tissue.

The anatomy of the Archaeocyatha was, therefore, quite unlike that of the Coelenterata, as in the absence of a coelenteron, food assimilation must have been taking place in the passages of the intervallum; it is also quite unlike the skeletons of the Porifera, which are made of spicules, and do not possess radial parieties, or laminar walls.

It is generally believed (Taylor, Vologdin, Okulitch) that the Archaeocyatha reproduced sexually by giving rise to freely swimming larva, which after a period of floating or swimming, settled on the bottom and secreted a skeleton of calcium carbonate. We may suppose that very soon after attachment (or just before as believed by Vologdin) the outer wall was secreted. The animal itself at this stage was a hollow

sack with an opening at the top and closely resembled a gastrula or olynthus stage. The primitive gastral cavity was in communication with the exterior by means of mural pores and the mouth. As the animal grew, first the outer wall and then the parieties were secreted. Later, by secretion of calcium carbonate at the inner tips of the parieties the inner wall was built. Occasional individuals among the Archaeocyatha have been shown to increase by budding and fission.

AFFINITIES

The dissimilarities from the Anthozoa can be tabulated as follows:

1) An inner perforate wall has no homologue in corals and is incompatible with anthozoan anatomy.
2) The inner cup or tube, in all probability was empty, the living animal occupying the loculi, and possibly only lining the outer and inner walls. It was, therefore, entirely different from the polyp of a coral.
3) The addition of parieties does not follow any regular plan. They may be added or subtracted haphazardly.
4) The parieties are not homologous to the septa of the Anthozoa.
5) All nepionic skeletons, and some adult genera, have no parieties at all.
6) The intervallum is of approximately constant width.
7) The tabulae of corals are imperforate; perforate in Archaeocyatha.
8) A great many Archaeocyatha do not resemble corals at all.
9) There is a tremendous time gap between the perforate Archaeocyatha and the oldest known perforate coral.

The similarities are very superficial, being in order of importance:

1) General conical or turbinate shape.
2) Presence of radial parieties or septa.
3) Substance of skeleton is made of compact calcium carbonate.
4) Young individuals have no inner wall.
5) Inner wall may be compared to a pseudo-columella or tube.

Vologdin (1937, p. 463) has expressed himself as follows: "With the corals, whose skeleton is just a framework for the living organism placed in it, the Archaeocyatha have no generic relationship. The external resemblance of Archaeocyatha and Rugosa is a case of convergence." Having become convinced that there is no relationship between the corals and the Archaeocyatha, Okulitch (1943) was forced to look for points of similarity with the only remaining possible phylum, the Porifera. These points of similarity were listed by him (Okulitch, 1943, p. 39). Professor de Laubenfels, having the advantage of his extensive knowledge of living sponges has examined these points of argument with the following results. Each of Okulitch's points is quoted below, verbatim and entire, within quotation marks. For each, however, explanatory comments are here added:

(1) "In general shape some of the Pleospongia greatly resemble *Archaeoscyphia minganensis* (Billings) an Ordovician sponge, and the calcareous and hexactinellid sponges." May we point out that *minganensis* is not a typical sponge in many ways. Just as vermiform shape is common to many genera in several phyla, so is the vasiform shape common to several phyla. It has survival value for sessile organisms in certain ecological situations.

(2) "The ontogenies of the Pleospongia and Porifera, especially the Calcarea, are similar, since both pass through a distinct *Olynthus* stage." May we point out that vague resemblances in extreme youth do not show close relationship. For example, ALL animals of ALL phyla pass through a zygote stage, and probably all could be said to pass through a morula stage. From there on, there are relatively few possible next steps. Many phyla proceed to blastula and gastrula, and are still separate phyla. The olynthus of sponges is positively not a true gastrula, but it is the equivalent or corresponding stage. The similar stage of Archaeocyatha may quite possibly have been a gastrula, or still a third type, neither a true gastrula nor olynthus, for all that the fossils reveal.

(3) "*Astrosclera willeyana* Lister and some pharetrones do not have a spicular skeleton but one made of calcareous spherules, which make a solid calcareous skeleton." Professor Okulitch is here led

astray by Minchin's chiefly excellent account of the Porifera in Lankester's "Treatise on Zoology." Yet hardly had this been published before it was discovered, that the original description of *Astrosclera* was utterly wrong. The organism in question is a symbiosis of a sponge with a coralline alga named *Rhododiplobia*, and the Archaeocyathea-like skeleton was made by the alga, and not by the sponge. For a reference on the exposure of the fallacy, one may see Kirkpatrick 1912, Proceedings of the Royal Society, B. volume 84, page 579. It seems clear that the misunderstanding about *Astrosclera* was a factor in the allocation of Archaeocyatha to Porifera.

(4) "Bedford mentions that 'the structural constituents of Archaeos range from laminae with or without occasional pores at one extreme to a network of what may be regarded as fused *spicular elements* at the other' (italics mine, V.J.O.)." May we call attention to the phrase "may be regarded," and point out that they should not be so regarded. As indicated in the quotation, the Archaeocyatha start out with a temporarily imperforate sheet in which foramina grow larger and larger until they are separated, in some cases, by only slender rods. The most nearly similar sponges have a vastly different history. The skeleton begins by widely-separated, needle-like spicules. These may be made in increasing number, and arranged so that they do not obstruct passageways, thus in some cases they finally arrive at a pattern of bars outlining windows. Let us call this structure "X." We may say then that sponges vary in many ways, and some of them, as they age, vary in the direction of "X." Also Archaeocyatha vary in many ways and some of them, as they age, vary in the direction of "X." Yet the beginnings for the two phyla are utterly different.

(5) "The skeleton is perforate." This is almost the repetition of Okulitch's point (4). May we point out again that the archaeocyathine skeleton begins as a sheet in which perforations appear, but that the sponge skeleton begins as discrete needles, which may in a minority of cases become cemented in such a way as to outline openings.

(6) "There is a fairly well-marked tendency towards loss of parieties and disintegration of skeleton." Similar losses occur in Mollusca, in Chordata, in many phyla. Such losses are not outstandingly characteristic of sponges at all. Furthermore, sponges never have any parieties to lose. The very existence of parieties shows that Archaeocyatha are not sponges.

(7) "The living animal resembled a sponge; there was a central paragastric cavity and a system of canals, leading from the exterior to the interior." May we point out that no man has ever seen the living archaeocyathine animal. The only available information is the observation by Okulitch (1946) that the skeletal elements of the intervallum are lined by a single thickness of cells, and that since the central cavity was in all probability empty, all the life functions were carried by the cells lining the passages of the intervallum. This is a sponge-like characteristic. Against this de Laubenfels argues that we do not know what the flesh was like. The flesh of the sponge is sharply characterized by flagellate chambers, with peculiar choanocytes. There is not the slightest evidence that such occured in the Archaeocyatha. The latter may have been ciliate rather than flagellate—may have pumped by muscular action, may actually have depended upon symbionts within them.

(8) "The fossils indicate the same variety of form as the sponges. This ranges from a slender cone to an irregularly folded bowl, or flat extension. The method of growth, therefore, probably was the same." May we point out that these shapes, universal in Archaeocyatha, occur in only a minority of sponges. These shapes also occur in coelenterates and some bryozoan colonies.

The basic dissimilarities between the Porifera and the Archaeocyatha can be summarized as follows: Sponges not only never have parieties, but never have inner and outer walls such as Archaeocyatha have. It is true that a very few fossil sponges seem to have stiffened cloacal walls, but these may be post-mortem artefacts. There is a cortex in a minority of sponges, but this is a region of multiplied spicules, not a wall. The granular-laminar skeleton of Archaeo-

cyatha is very different from the spicular skeleton of sponges, both in the method of development and in its over-all structure. The first known calcareous sponges occur in the Devonian; there is, therefore, a very long time gap between the calcareous Archaeocyatha of the Cambrian and the true Calcarea.

The reasoning presented above makes it impossible to include the Archaeocyatha in either the Porifera or the Coelenterata. The only remaining alternative is to propose a separate phylum for their special benefit. We believe that evidence for this is conclusive. It is further suggested that the name Pleospongea, being strongly suggestive of sponge affinity, be dropped and the name Archaeocyatha used for the phylum. The following outline of classification is suggested:

SUB-KINGDOM PARAZOA
PHYLUM ARCHAEOCYATHA
Class 1. Monocyathea
Class 2. Archaeocyathea
Class 3. Anthocyathea

MANUSCRIPT RECEIVED NOVEMBER 3, 1952

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PALEONTOLOGICAL NOTE

CORRECTIONS TO TRILOBITES IN "CAMBRIAN STRATIGRAPHY AND PALEONTOLOGY NEAR CABORCA, NORTHWESTERN SONORA, MEXICO"

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Since the manuscript of this paper was not available for correction after the publication by Franco Rasetti of "Middle Cambrian Stratigraphy and Faunas of the Canadian Rocky Mountains," Smithsonian Miscellaneous Collections, vol. 116, number 5, September 18, 1951, it is necessary that certain corrections and a discussion of some correlations be made now. The article mentioned in the title of this note appeared as Smithsonian Miscellaneous Collections, vol. 119, number 1, August 6, 1952.

Two typographical errors occur:—1) the titles of the two charts on pages 79 and 80 have been reversed. Thus chart 2 is on page 79 and chart 1 on page 80. An error has been made in the localities for *Zacanthoides* aff. *Z. holopygus* Resser. As noted in the discussion of the species on p. 143, specimens were obtained from only two localities, 800e′ and 801n. The following correction should be made:—on page 19 the occurrence in 801c with *Wanneria mexicana prima* should be deleted; on page 144, 801c should be deleted and on page 179, plate 30, figures 11 and 12 are both from loc. 801n.

Ptarmigania bispinosa Lochman, p. 133, is a species possessing the pygidial characters which Rasetti has made diagnostic of his new genus *Ptarmiganoides*. As Rasetti points out (1951, p. 179) the two genera are very close and because of the complete graduation in pygidial characters which I observed in the Langston material at the United States National Museum, I am doubtful whether *Ptarmiganoides* should have more than subgeneric status.

I am inclined to accept Rasetti's opinion that *Strotocephalus* Resser 1935 is a synonym of *Amecephalus* Walcott 1924. His material of *A. agnesensis* (Walcott) and *A. cleora* (Walcott) is complete enough to give an adequate picture of the close relationship of these species to the genotype, *A. piochensis* (Walcott). Thus *Strotocephalus arrojosensis* Lochman, p. 157, becomes *Amecephalus arrojosensis* (Lochman).

I have re-examined the several species referred to *Kochaspis* in view of Rasetti's new genus *Fieldaspis*. Rasetti indicates that the holotype pygidium of "*Crepicephalus*" *celer* Walcott undoubtedly belongs to *Fieldaspis*. The four cranidia from the Arrojos formation which I referred to as *Kochaspis* aff. *K. celer* (Walcott) should now be labeled "*Ptychoparia*" aff. "*P.*" *clusia* Walcott to indicate that the affinities are with that cranidium. Rasetti did not find any additional specimens of "*P.*" *clusia* and so could not correct the old generic determination. The two pygidia which I described as *Kochaspis cooperi* Lochman, though not well preserved, appear definitely to belong to *Kochaspis* rather than *Fieldaspis*.

Rasetti's work has demonstrated that there is probably one distinct faunal assemblage of Middle Cambrian age earlier than the *Albertella* zone which should be recognized in the standard section. Rasetti lists two zones, the *Wenkchemnia-Stephenaspis* zone and the *Plagiura-Kochaspis* zone, for his region, but I am inclined to agree with his more conservative suggestion (1951, p. 80) that "the differences observed are partly due to differences in facies between the corresponding stratigraphic intervals, and it would not be surprising to find in another area the genera here considered characteristic of the respective zones occurring together." The latter statement is undoubtedly the most correct for the Cordilleran area as a whole. J. F. Mason (1938) has listed a fauna containing *Kochiella, Kochaspis, Onchocephalus, Poliella* and *Plagiura* from the Highland Range, Nevada. These genera as well as *Ame-*

cephalus, Fieldaspis, Syspacephalus, Piazella and *Schistometopus* are to be expected associated in this earliest Middle Cambrian faunal assemblage. It should be noted that both *Amecephalus* in Montana and *Kochaspis* in Sonora are already known to extend into beds of the *Albertella* zone. *Oryctocephalus* and *Oryctocephalites* are known from sections in Utah and Idaho as well as the Canadian Rockies and appear to be characteristic of a more western, possibly deeper, part of the Cordilleran trough. This suggests that the closely associated genera, *Wenkchemnia* and *Stephenaspis*, will have a similar occurrence if they are found outside the Canadian Rockies. In the Sonora sections this earliest Middle Cambrian assemblage appears to be absent. At locality 801h, the base of the Arrojos formation, a small collection was obtained which might possibly represent a portion of this zone but since the two genera, *Amecephalus* and *Kochaspis?* identified from it are not entirely diagnostic of this zone but may extend into the *Albertella* zone, nothing more can be determined until a larger fauna has been collected.

On page 83 Rasetti is correct in assuming that the fauna of his *Bonnia-Olenellus* zone is the same as that of the *Antagmus-Onchocephalus* zone (Lochman, 1947). The genera of the Olenellidae appear equally abundant in each assemblage but the relative abundance of the early opisthoparian genera changes. Thus in the northern Cordilleran area as well as in the Appalachian areas *Bonnia* is quite conspicuous, whereas south of the Canadian Rockies the only *Bonnia* yet recorded is the single cranidium from locality 809a, and in the Sonora sections *Onchocephalus* is most abundant. Although Howell et al. (1944) attempted to recognize a post-olenellian *Syspacephalus* zone in the Lower Cambrian, I was forced to conclude that the faunal assemblage of the latter zone was the same as that of my *Antagmus-Onchocephalus* zone and consequently that the two zones were synonyms. Rasetti (1951, pp. 81–86) has thoroughly reviewed the various inaccuracies and inconsistencies involved in the *Syspacephalus* zone, and has demonstrated that *Syspacephalus charops* (Walcott), genotype and then only known species, is a normal member of his *Bonnia-Olenellus* zone, and that both *Kochiella* and *Inglefieldia*, also cited as dianostic of the *Syspacephalus* zone occur associated with Olenellidae.

Present knowledge of the Lower Cambrian indicates that in all areas of the Pacific Province *Olenellus* is the earliest trilobite to appear in the section, occurring either as the first fossil or else with or just above the first brachiopods or hyolithids, and persists as long as any genus of the Olenellidae; i.e., to the end of the Lower Cambrian as traditionally defined for the Cordilleran and Appalachian areas. Thus the entire Lower Cambrian should be correctly labelled the *Olenellus* zone to avoid any further misunderstanding.

At present only two valid subdivisions of this *Olenellus* zone can be recognized. 1) A lower subzone in which the various genera of the Olenellidae make their appearance and in which they are associated only with nontrilobitic forms such as primitive brachiopods, *Hyolithes, Salterella*, pleospongia and worm tubes. Near the base of any one Lower Cambrian section the brachiopod *Obolella* may make its appearance in marked abundance and the occurrence of such a bed gave rise to the designation of an *Obolella* zone. However, the occurrence of *Olenellus* with *Obolella* in the Proveedora Hills section, and the description of species of *Obolella* from all parts of the Lower Cambrian, indicates that a distinct pre-olenellian *Obolella* zone is not valid. Rather the sudden marked abundance near the base of many sections suggests the development of a favorable environment on the transgressing sea floor, a condition which will vary in time from region to region. 2) An upper subzone characterized by the association of the genera of Olenellidae with the Eodiscidae; genera of the Corynexochidae such as *Bonnia* and *Bonniella;* numerous small, generalized ptychoparids; several genera of the Zacanthoididae and a few other opisthoparian trilobite genera. The faunal assemblages of this upper subzone indicate that a number of opisthoparian families were well established before the Olenellidae died out.

Rasetti (1951, p. 82) suggested that the *Olenellus* zone (i.e. presumably any and all beds in which *Olenellus* and other genera of Olenellidae occur) may represent a shaly

facies of the Lower Cambrian deposits rather than a definite time interval and gives the northwestern Vermont section as an example. Such a suggestion was most reasonable at the time since not only in the Appalachian area but especially in the Cordilleran areas are there numerous thick sections of clastic sediments yielding (so far as present collections reveal) only an abundance of olenellid specimens. However, in the Sonora area the presence of *Olenellus* and *Wanneria* as the only trilobites throughout the limestones of the Puerto Blanco formation as well as in the overlying clastic Proveedora formation indicates that the earlier appearance of the Olenellidae in this Lower Cambrian sequence has a real time significance. It should be noted that the olenellid fossils from these formations consist entirely of fragmentary and weathered cephala and are very hard to obtain (Cooper et al., 1952, p. 4 and pls. 18, 19). The significance of the shaly facies seems to be one of preservation and not of ecology.

The faunal assemblages of the upper subzone do most frequently occur in dominantly carbonate beds but they are not restricted to this facies. At present more specimens of *Antagmus*, *Ptychoparella*, and *Periomma* are known from clastic than from carbonate deposits, and both *Bonnia* and *Periommella* occur in the sandy shales of York, Pennsylvania. Moreover, it should be noted that in these carbonate beds of the upper subzone the fragments of olenellids are as abundant as the specimens of the better preserved opisthoparian genera. When all sections throughout North America are considered there appears to be adequate evidence that these two subzones have a real time-stratigraphic significance.

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NOMENCLATURAL NOTES

THE NAMING OF CONODONT ASSEMBLAGES

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The Journal has recently published an extremely interesting and useful paper by F. H. T. Rhodes (1952, p. 886), in which he describes particularly lucid associations of conodonts. A. Scott Warthin and E. R. Eller have already written me, as chairman of the JCZNPA, asking an opinion of the legality of the nomenclature employed in this paper, and the problem involved seems important enough to warrant publication of some thoughts about it.

Rhodes decided that although individual conodonts had been named in the past these names applied to "form species" and "form genera" and that, with the additional information supplied by his assemblages, he was able to recognize and define "natural species," to which he gave new names. Thus, he erected the new genus *Scottella*, having as type species *S. typica*, defined on the basis of associations which included among other things jaws previously named *Streptognathodus elegantulus*, the type species of that genus. Was this action proper?

Let us go back to state some principles which are often overlooked or forgotten. A specific name in zoology applies to a species. Thus I may describe a footprint and give it a binomial name, but the name does not pertain to the footprint, but to the animal, otherwise unknown, which made it. When Stauffer and Plummer published the name *Streptognathodus elegantulus* they were not naming a tooth, but a species, and by their act *S. elegantulus* became the name of the species to which the animal belonged which had in its body the tooth they described.

If this is sound, then I think our answer is clear. We have the species *Streptognathodus elegantulus* which includes all animals considered to be conspecific with that which bore a certain tooth. We have the species *Scottella typica* which includes all animals conspecific with that which bore a tooth which, in the opinion of experts, is morphologically indistinguishable from this same tooth. In other words, we have two names for the same species of animal. This conclusion does not seem to be affected by the fact that we do not know what kind of animal this was, nor even if it used the tooth as a tooth, or by the fact that we now know that it had a lot of other teeth besides the kind originally described.

Thus I would see *Scottella typica* as a junior synonym of *Streptognathodus elegantulus* and *Duboisella typica* a junior synonym of *Metalonchodina bidentata*. *Illinella typica* seems objectively to be a junior synonym of *Illinella curvata* (Stauffer and Plummer), with the possibility of *Illinella* being a junior synonym of *Gondolella*, a matter for taxonomic judgment for which I am not competent (i.e. is *Illinella curvata* congeneric with *Gondolella elegantula*, the type species of that genus?). The other named conodonts recognized by Rhodes in his assemblages would drop their given names, for which there is no longer need, and e.g. the conodonts hitherto known as *Ozarkodina delicatula* would be referred to as the subbryantod element of *Streptognathodus elegantulus*. (I am here following Scott's terminology of 1942. It may be that conodont students would want to refine the terminology and call this an ozarkodine element, but that is unimportant for the present discussion.)

In all this I have been ignoring Rhodes' argument that the names of the separate conodonts are on a different level than those of the assemblages, and as "form species" may rightly be superseded by the new "natural" names. Let us now consider this question. It is true that from one point of view species based on isolated conodonts are "form species," but from that same point of view so also are species based on assemblages "form species." If names based on conodonts are to be suppressed when assemblages are found, are the names based on assemblages to be supressed in their turn

if specimens of whole animals turn up, in some freak preservation?

Possibly this argument will be clearer if we consider fossils other than conodonts. Frequently we have found pygidia before complete trilobites, teeth before complete skeletons of mammals, radials before complete crinoid thecae. Are we not agreed that in all such cases the proper name is that given to the first-named part of the animal? To argue that new names should be introduced when specimens are found permitting a more adequate definition of the species is to argue dangerously. A neontologist, on such grounds, could throw out all names of fossils, as being based on such trivia as bones, shells and teeth, and quite lacking the essential data on genitalia and nephridia needed for definition of "natural" species.

This question is rather peculiarly a paleontological one, for neontologists seldom name scraps of animals, whereas we do so all the time, and must, since we have only scraps, of greater or lesser size, to work with. Are our problems such that we should ask the International Commission for some sort of special dispensation in the rules? I do not think so, personally, but would be glad to pass on to the Commission any suggestions which may be made. The Commission held, in Paris, that any names we may wish to give to scraps under a utilitarian classification would not come under the operation of the *Règles*, but that if we refer material to genera and species then we must abide by the rules governing the naming of genera and species. There is no difference between a species in paleontology and a species in ornithology. Each is a group of animals with a history, a geographic range, an ecologic preference, the individuals in it having ontogenies, and bodies with morphological and physiological characteristics. It is true that we know much more about a species of bird than a species of conodonts, can define it more accurately, can describe it more fully, but the species itself should still have a meaning apart from our knowledge of it.

These are matters of taxonomy, and nomenclature only enters in to say: A species may have only one name. If, with increase in knowledge, it becomes apparent that more than one name has been applied to the same species, then the proper name for the species is that first proposed for it, regardless of what anatomic material or developmental stage induced the student to propose it, for he was not naming his material, but the species to which it belonged.

This note represents my own opinions, only, but members of the Committee are being asked to comment if they feel that I have not properly expressed the case.

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THE TYPE SPECIES OF *ACULEODISCUS* AND THE STATUS OF *DAWSONIA* (CAMBRIAN TRILOBITES)

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The recent erection of a new genus of Cambrian trilobites, *Aculeodiscus* (Šnajdr, 1950, p. 201) raises a question of nomenclatural practice which calls for comment, the more so since this genus would seem to be either a synonym of, or an acceptable substitute for, the disputed name *Dawsonia*.

Aculeodiscus has as type species by original designation, the new species *A. bohemicus* Šnajdr. This species, as interpreted by its author, has two sections which he treats as subspecies under the names *A. bohemicus bohemicus* Šnajdr 1950 and *A. bohemicus dawsoni* (Hartt [in Dawson 1868]).

This usage is, I think, inadmissible. If two nominal species are united, as Šnajdr has united *Aculeodiscus bohemicus* Šnajdr and *Microdiscus dawsoni* Hartt, then the combined species must bear the older of the two names, if it is available. Accepting with-

out comment Šnajdr's synonymy, then we would have a species *Aculeodiscus dawsoni* (Hartt in Dawson), with two subspecies *A. dawsoni dawsoni* and *A. dawsoni bohemicus* (Šnajdr).

The type species of the genus must be *A. dawsoni* to any author who agrees that *A. bohemicus* and *Microdiscus dawsoni* are conspecific. The junior status of the name *bohemicus* depends on this subjective synonymy, and an author who felt that the Canadian and the Bohemian forms were specifically distinct would consider the name of the type species to be *A. bohemicus*. (The type species itself is the same throughout: all this talk is of the name of that species.) I would suggest to my Czech colleague that he consider whether it might not be expedient, for the sake of clarity in terminology, to consider these forms as closely related but distinct species, an interpretation which would permit retention of the trivial name *bohemicus* as that of the type species of the genus.

Since *Microdiscus dawsoni* is the type species of the genus *Dawsonia* some comments on this generic name may be in order. The Richters (1941, p. 21) have held that *Dawsonia* was not validly published in 1868. Rasetti (1952, p. 436) has held that it was so published. The *Règles* are by no means clear on this point, but until they are clarified I would agree with Rasetti. The facts as I see them are these: Dawson (1868, p. 654–655) published the species *Microdiscus Dawsoni*, the description being taken from Hartt's manuscript. To Hartt's description Dawson added "Note.—Mr. Hartt had originally described this species under the new generic name of *Dawsonia;* but Mr. Billings regards it as a species of *Microdiscus* of Salter." This I take to be publication of the name *Dawsonia* in synonymy, as much as if Dawson had headed his description "*Microdiscus dawsoni* (syn. *Dawsonia dawsoni*)." Presumably the whole question of publication in synonymies will be considered at the meeting of the International Commission in Copenhagen this Summer, and a definite ruling given for our guidance.

The name *Dawsonia* was certainly published for this trilobite by Matthew (1896, p. 29), but by that date the name had been proposed by Nicholson for another organism.

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NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

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